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Malacological Review, 1977, 10: 1-6

REVIEW OF CURRENT LITERATURE ON THE ECOLOGY AND EXPLOITATION OF THE EDIBLE SNAIL *HELIX POMATIA*

Joan M. Welch and E. Pollard

ABSTRACT

Helix pomatia is of topical interest because the increasing scale of exploitation has given rise to fears of serious depletion to wild populations. The literature is widely scattered and, therefore, this paper brings together publications since 1950 which relate to the ecology and exploitation of this snail. The paper covers over 60 publications in 10 languages, and the authors give brief comments on the scope and value of each.

Helix pomatia Linnaeus, variously known as the edible, Roman, apple or vineyard snail, is of economic importance in many European countries, and the literature on its ecology and exploitation is widely spread throughout Europe. However, during the course of our work, we have noticed that authors frequently seem to be unaware of many of the publications on this species outside their own countries. As we have suggested that a greater degree of ecological knowledge is necessary in order to exploit this snail without undue damage to the wild populations, we hope, in producing this review, to give future workers a broad base of known information.

We have confined ourselves, with a few exceptions, to work published during the last 25 years. In general, earlier papers are referred to by later authors or else their findings have been superseded by more detailed or more authoritative studies.

We have divided the review into 4 broad categories. Many of the publications cover more than 1 category, but we have allocated to the dominant one where possible. Some are sufficiently broadly based to be termed 'general.'

General

Many of these publications are reviews which concentrate on studies in the language of the author.

CADART, J. 1955. 2nd ed., 1975. Les escargots (*Helix pomatia* L. et *Helix aspersa* M.) biologie, élevage, parcage, histoire, gastronomie, commerce. *Savoir Hist. natur.*, (24): 1-436. Paul Lechevalier, Paris.

A monograph. The sections on history and folklore are a feature of the book, and exploitation, in France particularly, is covered in detail, but the biological information is largely anecdotal.

FRÖMMING, E. 1954. *Biologie der mitteleuropäischen Landgastropoden.* Duncker Humblot, Berlin. 404 p.

Includes a detailed section on *Helix pomatia*, with valuable information on feeding. The book contains many references to earlier publications, particularly the author's own considerable work, on this snail.

HEIN, G. 1952. Die Weinbergschnecke (*Helix pomatia* L.). Lebensweise, Verbrauch, Handel und Zucht. *Z. hyg. Zool.*, 40: 225-248.

A fairly comprehensive review of information, mainly from Germany.

KILIAS, R. 1960. *Weinbergschnecken. Ein Überblick über ihre Biologie und wirtschaftliche Bedeutung.* VEB Deutscher Verlag der Wissenschaften, Berlin. 94 p.

A monograph; predominantly anatomy, physiology and morphology. It is very

detailed with many diagrams. The section on exploitation is relatively small. Many references.

MEISENHEIMER, J. 1912. *Die Weinbergschnecke* Helix pomatia *L.* Monographien einheimischer Tiere, Vol. 4. Werner Klinkhardt, Leipzig. 140 p.

An older publication dealing mainly with physiology and morphology, but we include it here because it is the first comprehensive study.

NIETZKE, G. 1963. *Die Weinbergschnecke.* Eugen Ulmer, Stuttgart. 163 p.

A semi-popular book covering the whole area of information on *Helix pomatia,* drawn mainly from German sources. It has useful detail on distribution and exploitation.

TAYLOR, J.W. 1907-1914. *Monograph of the land and freshwater Mollusca of the British Isles.* Vol. 3. Taylor Bros., Leeds. 522 p.

Included because it is the only publication at present which discusses English distribution in detail. A large part of the extensive section on *Helix pomatia* deals with the named variations which so concerned early workers.

Ecology

This category covers those publications which are mainly ecological or contribute to ecological knowledge.

AGÓCSY, P. 1963. The examination of some edible snail (*Helix pomatia* L.) populations (Mollusca). *Ann. hist.-natur. Mus. natn. hung.,* 55: 513-520.

A comparison of 12 Hungarian populations in terms of shell size. Considerable variation reported,but no statistical analysis.

AGÓCSY, P. 1966. Néhány éticsiga populáció vizsgáláta. *Állatt. Közl.,* 53: 13-19. [German summary.]

Essentially the same information as the previous paper.

ANDREIKEVIČ, E. 1969. Biologija rezmnozhenija vinogradnoj ulitki v litve. *Liet. TSR Mokslų Akad. Darb.,* ser. B, 1(48): 111-117. [Lithuanian and English summaries.]

Reproductive biology of a marked population observed over 3 years. Comments on USSR distribution.

EDELSTAM, C. & PALMER, C. 1950. Homing behaviour in gastropods. *Oikos,* 2: 259-270.

Includes studies on the snails' ability to return to their hibernating sites.

FLORACK, P. 1952. Roman snails and the weather. *Weather,* Lond., 7: 289-290.

Brief popular article.

LIND, H. 1968. Hibernating behaviour of *Helix pomatia* L. (Gastropoda. Pulmonata). *Vidensk. Medd. dansk naturhist. Foren.,* 131: 129-151.

A very detailed study.

LIND, H. 1973. The functional significance of the spermatophore and the fate of the spermatozoa in the genital tract of *Helix pomatia* L. (Gastropoda. Stylommatophora). *J. Zool.,* 169(1): 39-64.

A very detailed study. Gives an explanation for post-mating behaviour.

ŁOMNICKI, A. 1964. Some results of experimental introduction of new individuals into a natural population of the Roman snail, *Helix pomatia* L. *Bull. Acad. pol. Sci.,* Cl. II., Sér. Sci. biol., 12: 301-304.

Differences in behaviour of introduced and resident individuals observed and discussed.

ŁOMNICKI, A. 1969. Individual differences among adult members of a snail population. *Nature,* Lond., 223: 1073-1074.

Variability in number of recaptures of individuals during mark and recapture work on a specific population. The conclusions drawn and the analysis of results are disputed by Pollard (1973, 1975a).

ŁOMNICKI, A. 1971. Struktura i regulacja wielkości populacji ślimaka winniczka, *Helix pomatia* L., a niektóre zagadnienia jego ochrony. *Ochr. Przyr.*, 36: 189-255. [English summary.]

The first major work devoted to the ecology of the edible snail, but the population data are insufficient to support all the conclusions. Suggests a need for legislation to control exploitation.

ŁOMNICKI, A., WĄSILEWSKI, J. & KOSIER, A. 1964. Metoda i wstępne wyniki badań nad populacja ślimaka winniczka *H. pomatia* L. *Ekol. pol.*, ser. B, 10(2): 106-112. [English summary.]

The methods used to study snail populations are explained. Includes preliminary results.

LUNDQVIST, G. 1966. Till molluskernas biologi II. *Fauna Flora*, Upps., p 102-108.

Observations on 1 snail in a garden population over a period exceeding 30 years!

POLLARD, E. 1973. Growth classes in the adult Roman snail (*Helix pomatia* L.). *Oecologia*, 12: 209-212.

A means of separating adults into growth classes is outlined.

POLLARD, E. 1975a. Aspects of the ecology of *Helix pomatia* L. *J. anim. Ecol.*, 44: 305-329.

Distribution and habitat in England are discussed. Further studies on the growth/age classes of adults. Detailed ecological studies of an isolated English population with supporting experimental work.

POLLARD, E. 1975b. Differences in shell thickness in adult *Helix pomatia* L. from a number of localities in southern England. *Oecologia*, 21: 85-92.

Differences in shell thickness between populations appear to be genetic and can be related to rainfall variation.

TISCHLER, W. 1973. Zur Biologie und Ökologie der Weinbergschnecke (*Helix pomatia*). *Faun.-Ökol. Mitt.*, 4: 283-298. [English summary.]

Population ecology studies based on a garden site. Three years detailed study supported by 15 years knowledge of site. Effect of light, diurnal rhythms, home range, effect of introductions, also reported.

TISCHLER, W. 1974. Aussenfaktoren als Auslöser tageszeitleichen Verhaltens und begrenzter Dormanz bei *Helix pomatia* L. *Zool. Anz.*, Jena, 193(3/4): 251-255. [English summary.]

Experiments with juveniles proving that external factors rather than internal rhythms determine activity.

TURČEK, F. 1970a. Studies on the ecology and production of the Roman snail, *Helix pomatia* L. *Biológia*, Bratisl., 25(2): 103-108. [Polish summary.]

TURČEK, F. 1970b. Growth in the early juvenile Roman snail, *Helix pomatia* L. and secondary netto production. *Biológia*, Bratisl., 25(8): 555-558. [Polish summary.]

The 2 papers above by Turček cover studies undertaken as part of an International Biology Programme-Productivity Terrestrial programme. The observations show little understanding of the ecology of the snail.

TURČEK, F. 1974. Reštitúcia slimáka záhradného *Helix pomatia* L. rozličného veku po hladovaní. *Biológia*, Bratisl., 29(5): 417-421. [English and Russian summaries.]

Observations on the rejection of unpalatable food.

TURČEK, F. & TURCEKOVA, Anna. 1973. Variabilita váhy, sušina tela, konzumpcia detritu lístia drevín a niektoré ekologické poznámky o *Helix pomatia* L. *Biológia*, Bratisl., 28(8): 665-669. [English and Russian summaries.]

Observations on feeding and weight changes. As in the above papers by Turček, the ecology of the snails appears to be little understood and there is little reference to other workers.

URBAŃSKI, J. 1963. Ślimak winniczek *Helix pomatia* L. - jego systematyka, biologia, znaczenie gospodarcze i ochrona. *Ochr. Przyr.*, 29: 215-254. [Long English summary.]
A very detailed study. The wealth of literature on variations and the author's own studies on museum and live material is discussed and the taxonomy clarified. The need for more detailed ecological studies is suggested in reference to formulating legislation to control exploitation. Many references to earlier workers.

Distribution and introductions

We have put in this category those publications which include international, national or detailed local studies. In general, we have excluded those which deal only with casual observations or individual sites. Many of the countries where *Helix pomatia* occurs have a published faunal list readily accessible, so we have also excluded those publications from this list.

ANT, H. 1957. Die Weinbergschnecke in Westfalen. *Natur & Heimat*, 17: 104-108.
Includes size comparisons.

BUTOT, L.J.M. 1970a. Geschiedenis en stand van de Wijngaardslak in Friesland. *Levende Natur.*, 73: 40-46. [English summary.]

BUTOT, L.J.M. 1970b. Antoni van Leeuwenhock en zijn "Wijngaart Slakken." *Levende Natur.*, 73: 172-182. [English summary.]

BUTOT, L.J.M. 1970c. De geschiedenis en de verspreiding van de Wijngaardslak in 's-Gravenhage. *Levende Natur.*, 73: 275-282. [English summary.]

BUTOT, L.J.M. 1972. De geschiedenis en de verspreiding van de Wijngaardslak langs de duinzoom. *Levende Natur.*, 75: 29-40. [English summary.]

BUTOT, L.J.M. 1973. De geschiedenis en de verspreiding van de Wijngaardslak in de beide Hollanden, Noordbrabant, Zeeland en Utrecht. *Levende Natur.*, 76: 166-179. [English summary.]

BUTOT, L.J.M. 1974. De geschiedenis en de verspreiding van de Wijngaardslak in de oostelijke en de noordelijke provincies van Nederland. *Levende Natur.*, 77: 166-180. [English summary.]
The 6 papers above by Butot cover the history and distribution of *Helix pomatia* in Holland. Investigations have been made on the history of individual populations. Comments on exploitation and legislation.

DEES, Lola T. 1970. Edible land snails in the United States. *U.S. Dept. Interior Res. Publ.*, 91: 1-8.
Helix pomatia included as an introduced species. Brief note on distribution in U.S.A.

LEWIS, E. 1964. The survey of *Helix pomatia*. *Proc. Trans. Croyden natur. Hist. sci. Soc.*, 13: 185-190.
A fairly comprehensive survey of distribution in the Southeast of England.

POLLARD, E. 1974. Distribution maps of *Helix pomatia* L. *J. Conchol.*, 28: 239-242.
A method of mapping using English records which highlights the true centres of distribution.

TURNER, R.D. 1961. *Helix pomatia* colonised at Plymouth, Mass. *Nautilus*, 74: 122.
Brief note.

VAN DER SCHALIE, H. & DUNDEE, D.S. 1958. *Helix pomatia* colony at Jackson, Michigan. *Nautilus*, 72: 16-18.
An introduced population.

WALDEN, H. 1955. The land gastropods of the vicinity of Stockholm. *Ark. Zool.*, 7: 391-449.
Comment on man as the distributing agent.

Exploitation

This category covers farming, collecting, extinction through over-collecting, legislation to control collecting and conservation measures. We have adopted the French words 'parcage' and 'élevage' as being more descriptive than the word farming. The former involves keeping wild snails in captivity until required and the latter maintaining and culling a captive breeding population.

CHEVALLIER, H. 1973a. Les mollusques continentaux de France d'intérêt économique. *Haliotis,* 3: 9-18. [English summary.]

Factual report which includes *Helix pomatia* and related species.

CHEVALLIER, H. 1973b. Répartition en France et importance économique de l'escargot de Bourgogne, *Helix pomatia* Linné. *Haliotis,* 3: 177-183. [English summary.]

Includes a map showing distribution in France pre- and post-1950 and a list of countries in which the snail occurs. Draws attention to the need for legislation in France.

CHEVALLIER, H. & DUFOURNET, P. 1974. L'escargotière du gisement Gallo-Romain de Seyssel (Haute-Savoie). *Bull. Mus. Hist. natur. Marseille,* 34: 167-174.

Reconstruction of age structure of a Franco-Roman snail farm from measurements of excavated shells.

DUBOURG, A. 1969. Elever des escargots . . . . . pourquoi pas? *Encyclopédie des Connaissences Pratiques.* Biscaye Fréres, Bordeaux. 86 p.

A small book on snail 'élevage,' but it does not provide convincing evidence of commercial viability. Mostly a vehicle for pursuing the author's views against any intensive farming methods in agriculture today.

GALLO, G. 1954. L'allevamento della lumachi. *Italia agr.,* 91(10): 749-758.

Popular article.

GALLO, G. 1960. *L'allevamento della chioccola.* Edizioni Agricole, Bologna. 126 p.

Predominantly snail exploitation referring to France and Germany, but covering Italian information.

JUNGWIRTH, F.J. & NAWRATIL, O. 1970. *Die Praxis der Weinbergschneckenzught* Helix pomatia. *Ein im Entstehen begriffener Erwerberbszweig.* Jungwirth, Hausen/Kill. 58 p.

A duplicated commercial publication of snail farming, using snails and equipment bought from the authors' firm. Quite detailed and draws attention to the need to conserve wild populations. Most recent of several similar publications.

JUTTING, W.S.S. van Benthem. 1952. A snail farm in the Netherlands. *Basteria,* 16: 25-30. [Dutch summary.]

Secondhand report of casual observations.

LECOMTE, V. 1973. Le marché des mollusques en France. *Haliotis,* 3: 173-175.

Details of snail imports into France 1969-1971 and exports 1970-1971.

MAGLIANO, A. 1964. L'allevamento della chiocciola. *Italia agr.,* 101(11): 1139-1162.

Fairly comprehensive popular article. Some information on preferred aspect.

MEYNADIER, G., BAGOIN, M. & VAGO, C. 1964. Bacteriose epizootique chez les Helicides (Mollusques). *Antonie van Leeuwenhoek,* 30: 76-80.

Details of a bacterial disease which kills snails raised in artificial conditions. This is the only work of this kind, although a disease is frequently mentioned by other workers.

NAWRATIL, O. 1969. Probleme der Massenvermehrung von *Helix pomatia* L. *Malacologia,* 9(1): 135-141.

Discusses increasing demand for snails and lack of success in farming. Comments on unexplained disease affecting snails under farming conditions. Gives a long list of references, mostly unobtainable because they are personal typed documents.

NAWRATIL, O. 1970. Odomashivanije vinogradnoj ulitki. *Priroda*, Mosk., 11: 96-97.
Translation of a popular article in German into Russian.

PASTORINI, F.M. 1961. Contributo allo studio dell'elicicoltura. Osservazioni rilevi ed elaborazioni sugli allevamenti della Valli Cuneesi nei loro aspetti zooeconomici. *Riv. Zootec.*, 34: 211-212; 214-215; 217-219.
A detailed account of the first farming attempt in Italy. This is 'parcage' rather than 'élevage.'

POPESKOVIC, D., ŽIVANOVIĆ, D. & MUČALICA, Z. 1964. Vinogradski puž (*Helix pomatia* L.) kao hrana i izvozni materijal. *Vet. Glasn.*, 18: 1157-1158.
Brief account of exploitation with collecting methods and useful figures.

PRUDHOMME, M. 1960. Les escargots. *Rev. Méd. vét.*, 23: 456-461.
Popular review article. Quotes Cadart extensively.

SOÓS, L. 1936. Az ehető csiga életmódja és tenyésztése. *Természettud. Közl.*, 68: 1-4.
An older paper but included as it is not referred to by many workers. It covers exploitation in Hungary, draws attention to problems and dangers of over-collecting *Helix pomatia* and related species.

THEVENOT, A. & LESOURD, F. 1974. *L'escargot et la grenouille comestibles.* La Maison Rustique, Paris. 96 p.
The source of frequently reproduced diagrams of snail farms. The section on 'parcage' is very detailed, but that on 'élevage' speculative. Gives details relating aspects of exploitation and suggests need for scientifically sound legislation.

VÁSÁRHELYI, I. 1963. Az éticsiga gyűjtéséről. *Állatt. Közl.*, 52(1-4): 143-146.
Whilst demonstrating the value to the country of snail exports, the author draws attention to the need for controlled collection.

WELCH, Joan M. & POLLARD, E. 1975. The exploitation of *Helix pomatia* L. *Biol. Conserv.*, 8: 155-160.
Review of current situation in Europe from literature and correspondence.

WILDHABER, R. 1950. Schneckenzucht und Schneckenspeise. *Schweiz. Arch. Volksk.*, 46(3/4): 119-184.
A review of the literature on the history and practice of eating snails. Six pages of references.

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Malacological Review, 1977, 10: 7-13

ECOLOGICAL FACTORS INDUCING ESTIVATION IN THE FRESHWATER LIMPET *FERRISSIA WAUTIERI* (BASOMMATOPHORA: ANCYLIDAE). I. OXYGEN CONTENT, ORGANIC MATTER CONTENT AND pH OF THE WATER

Monique Richardot

ABSTRACT

It has been stated previously that the septifer form in *Ferrissia wautieri* is a drought resistant form. The precise conditions which favor development of septa are now defined. When the water temperature is high (25°C) and the photoperiod is 16 hours light, the main factor responsible for septum development is the chemical quality of the water – anoxy linked with a high organic matter content.

INTRODUCTION

Ferrissia wautieri is a freshwater limpet of ponds and stagnant waters. It lives on immersed *Typha* leaves, as well as other decaying vegetation, eating periphyton (Favier-Gamulin, 1969). These limpets are hermaphroditic and capable of self-fertilization.

In *Ferrissia wautieri* all hatching juveniles are typical ancylids, but after hatching their development may proceed in 2 different ways. Either the individual grows and then reproduces without changing the shape of the shell, or the animal develops a septum before it starts to breed. The septum is a thin calcareous layer partially closing the shell aperture. Later the animal forms a new shell from the edges of the constricted aperture. On following the 1st course, the limpet retains the ancyloid shape throughout life; on following the 2nd course, the limpet passes through 3 successive stages: ancyloid, septifer and postseptifer (Wautier et al., 1962).

Numerous observations made in the natural habitat indicate that the septifer form is a drought resistant form (Richardot, 1974, 1976). We are now able to define the ecological conditions which favor septum development.

Immature individuals begin to develop a septum when the mud is still covered by a thin layer of water, just before drought. When this remaining water evaporates, the limpets go into the wet mud and complete their septum. They survive, there, in the wet mud, estivating until the water level rises again. As favorable conditions return, the limpets leave the mud and appear again on the immersed *Typha* leaves. They then start to form a new shell (postseptifer form) and the first laying takes place.

Thus, the septifer form is a drought resistant form, although it is not exactly the drought which triggers off the septum formation, but the physical and chemical variations of the water quality. When the water level is decreasing, diurnal temperatures rise, the oxygen content and the pH generally decrease, and the organic matter content increases (Richardot, 1974, 1976).

In order to establish the ecological factors which are involved in determining septum formation, several experiments were performed in the laboratory. The experiments discussed in the present paper deal with the role of 3 factors: oxygen content, pH and organic matter content of the water.

METHODS

Two series of experiments were carried out, each one with 12 groups of limpets.

The initial breeding conditions were identical in the 24 jars (375 ml glass). In each jar, 40 new hatchling juveniles were immersed in water (250 ml) with a piece of *Typha* leaf. The jars were covered with a transparent plastic sheet. The water temperature was maintained at 25°C. The photoperiod was 16 hrs light. The spatial variation in light intensity was 600-900 lux.

Food (*Typha* leaves) and water, both collected in the natural habitat, were replenished at weekly intervals.

Experiment 1

Three rearing methods were compared with regard to the septifer percentages obtained after 6 and, in some cases, 11 weeks:

Method A – each time food (the *Typha* leaf with its epiphyton) and water were removed, they were replaced by 250 ml of water and another piece of *Typha* leaf. Thus, the water in the jar was new each week and it contained only 1 piece of *Typha* leaf.

Method B – each week the water was replaced and a new piece of *Typha* leaf was added.

Method C – the water of the jar was never replaced, but each week a new piece of *Typha* leaf was added.

Experiment 2

The methods B and C above were compared with method D below:

Method D – the water of the jar was never renewed, but each week the piece of *Typha* was removed and replaced.

Data concerning septifer percentages, shell lengths, pH (taken by pH meter) and the oxygen content (determined by oxymeter) of the water were recorded 6 weeks later. The 120 animals (40 x 3) of each group of 3 jars (M_1, M_2 and M_3, for example) were kept from the same strain. For each food distribution, 3 equal parts of the same *Typha* leaf were put in the 3 jars of one group.

Experiment 3

The organic matter content of the water was determined by titration with potassium permanganate. This method permitted a rough estimate of the organic substances in the water. The water samples required by this method had to be different according to the quantity of organic matter dissolved; the richer the water with organic matter, the smaller the sample required.

One experiment was carried out to investigate the variation in accumulation of organic substances in the water of the jar according to the rearing method used. Since method A called for removal of the water each week, the accumulation of organic substances was impossible, so Experiment 3 was performed only for methods B, C and D.

The experimental scheme was similar to that of Experiment 2, but no animals were kept in the jars. Therefore, the organic matter had only a vegetal origin. Three equal parts of the same leaf were put each week in the 3 jars of one group (B_1, C_1, D_1) (temperature 25°C, photoperiod 16 hrs light). For the titration of the water samples, 10 ml were diluted in 90 ml of distilled water. Each measurement represented the medium of 2 titration results.

Experiment 4

Experiment 4 was performed to investigate the accumulation of organic substances in the water in the case of rearing method C. Six groups of 2 jars were used, each with 250 ml of water and the same surface of *Typha* leaf (the pieces of *Typha* for the 2 jars of each group came from the same leaf). No animals were kept in the jars. The water in the jars was never replaced, but each week a new piece of *Typha* leaf was added (method C) (temperature 25°C, photoperiod 16 hrs light). Each week the water

of the 2 jars of a group was analysed and the jars eliminated. Two titrations were performed for 1 measurement. Each measurement represented the medium of 2 titration results. As the accumulation of organic substances increased, the water samples were reduced: 50 ml, 20 ml and 10 ml, diluted in distilled water to make up 100 ml.

Statistical methods

Septifer percentages were calculated with regard to the number of living individuals which were 1.29 mm long or more (1.29 mm is the length of the smallest septifer obtained in the laboratory or collected in the natural habitat in 10 years; Fig. 1). Thus, the data obtained took into account all individuals (1st and 2nd generations) which had reached or overtaken the period of septum development.

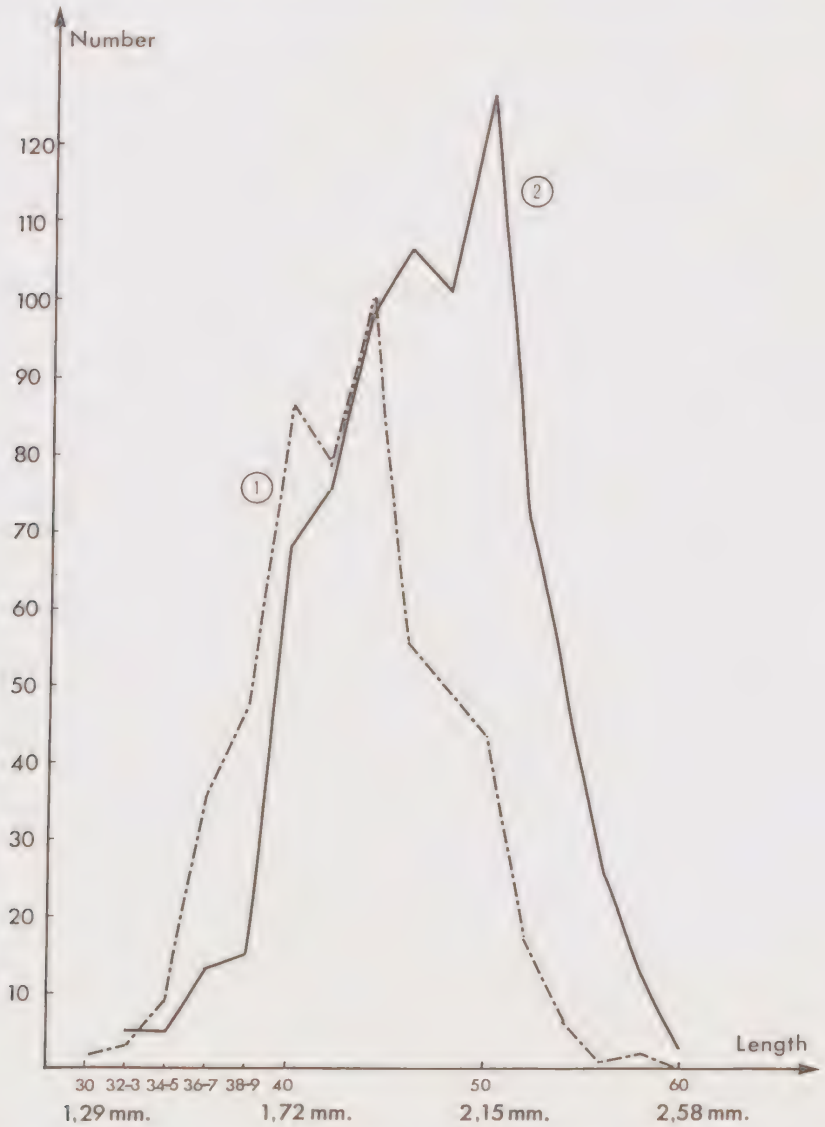

FIG. 1. Lengths of estivating *Ferrissia*. 1 – septifers collected in their natural habitat; 2 – septifers obtained in the laboratory.

TABLE 1. Experiment 1; comparison between rearing methods A, B and C.

Jar	R	A	No. ancyloid j	s	m	S	Total animals s + m	%	pH	O_2
Week 6										
1	A	16	2	8	5	1	14	7.1	7.5	5.75
2	B	103	70	12	7	14	33	42.4	7.2	2.75
3	C	81	60	7	3	11	21	52.3	7.2	1.80
4	A	42	19	20	3		23	0	7.6	5.75
5	B	39	9	25	5		30	0	7.2	2.30
6	C	37	1	19		17	36	47.2	7.2	1.50
7	A	40	15	18	7		25	0	7.5	5.70
8	B	98	67	18	6	7	31	22.5	7.2	3.25
9	C	59	21	6	3	29	38	76.3	7.2	2.35
10	A	19	2	12	5		17	0	7.4	4.60
11	B	44	16	20	7	1	28	3.5	7.2	2.65
12	C	29	1	13	3	12	28	42.8	7.1	1.80
Week 11										
4	A	234	220	6	8		14	0	7.3	4.80
5	B	121	92	18	10	1	29	3.4	7.1	1.60
6	C	104	66	4	10	24	38	63.1	7.3	1.80
7	A	124	112	4	8		12	0	7.5	5.30
8	B	107	76	12	14	5	31	16.1	7.1	1.90
9	C	134	57	31	3	43	77	55.8	7.3	1.70
10	A	24	10	8	6		14	0	7.6	5.90
11	B	122	82	25	8	7	40	17.5	7.1	1.90
12	C	103	69	5	10	19	34	55.8	7.3	1.20

R – rearing method; A – total number animals; j – juveniles which were less than 1.29 mm long; s – submature individuals which were less than 2.58 mm long; m – mature individuals which were more than 2.58 mm long; S – number of septifers; % – septifers percentage.

The experimental data (septifer percentages obtained with the different methods) were analysed with nonparametric tests (Siegel, 1956): the Mann-Whitney U test and the Kruskal-Wallis H test. The Spearman rank correlation coefficient was used to measure the correlation between the septifer percentages and the chemical qualities of the water.

Results

The septifer percentages were significantly different (H = 6.16; significant for P = 0.05) for the 3 rearing methods A, B and C at the end of week 6 in Experiment 1 (Table 1). Method A was not favorable, whereas the number of septifers was significantly higher with method C than with method B (U = 0). The 2nd generation subjects were small, thus probably all the estivating individuals belonged to the 1st generation. The efficiency of method C was confirmed by the data obtained after 11 weeks (Table 1). Some individuals belonging to the 2nd generation were then old enough to develop a septum. (M_9).

In Experiment 2 (Table 2), the septifer percentages were highly different (P = 0.01) for the 3 methods of rearing (H = 8.11). The results clearly show the efficiency of method C (for B and C, U = 0, significant for P = 0.01; for D and C, U = 1, significant for P = 0.02).

The Kruskall-Wallis H test applied to the pH data (Tables 1 and 2) showed that the pH was not affected by the different rearing methods A, B, C and D. Consequently, there is no correlation between the water pH and the septifer percentages. With regard to the water oxygen content, the data obtained with rearing method A were significantly higher, and there was a positive correlation between the water oxygen content and the septifer percentages in Experiment 1 whereas this correlation is absent in Experiment 2.

Experiment 3 showed that method C lead to a larger accumulation of organic substances in the jars (Table 3). The results of Experiment 4 illustrate the rate of this accumulation through 6 weeks (Table 4); the content of organic substances may be 7 times more after 6 weeks.

TABLE 2. Experiment 2; comparison between rearing methods B, C and D.

Jar	R	A	No. ancyloid j	s	m	S	Total animals s + m	%	pH	O_2
13	B	207	169	17	19	2	38	5.2	7.2	1.9
14	C	50	19	14	4	13	31	41.9	7.2	2.1
15	D	48	18	18	4	8	30	26.6	7.5	5.1
16	B	138	116	3	14	5	22	22.7	7.3	2.1
17	C	50	20	6	5	19	30	63.3	7.2	1.8
18	D	74	47	12	3	12	27	44.4	7.3	2.3
19	B	56	23	9	16	8	33	24.2	7.1	1.9
20	C	65	33	1	5	26	32	81.2	7.2	2.45
21	D	69	41	14	6	8	28	28.5	7.2	3.0
22	B	179	144	16	10	9	35	25.7	7.2	2.5
23	C	68	32	5	4	27	36	75.0	7.1	2.4
24	D	52	23	18	4	7	29	24.1	7.4	4.2

R – rearing method; A – total number animals; j – juveniles which were less than 1.29 mm long; s – submature individuals which were less than 2.58 mm long; m – mature individuals which were more than 2.58 mm long; S – number of septifers; % – septifers percentage.

TABLE 3. Experiment 3; comparison of the organic matter content of the water between rearing methods B, C and D at week 6.

Jars	Organic matter content* mg 0_2/l	Jars	Organic matter content* mg 0_2/l
B_1	17	B_2	20
C_1	32	C_2	45
D_1	18	D_2	30

*Organic matter content of the water at time 0 = 4.6 mg 0_2/l.

DISCUSSION

It is generally assumed that the food quantity available plays a role in growth and reproduction (Mooij-Vogelaar et al., 1973; Mooij-Vogelaar & Steen, 1973). In Experiments 1 and 2, the experimental set-up involved may lead to somewhat of a discrepancy in respect to the food quantity and to some rearing conditions between the jars of methods A, B, C and D.

The set-up of Experiments 1 and 2 implied large differences in the food supply in the jars of methods A, B, C and D. So, the restrictive diet (one piece of leaf) in jars A and D probably involved a partial starvation for the 40 animals. On the other hand, the progressive accumulation of pieces of *Typha* leaves in the jars of methods B and C ensured a larger food supply.

The rearing methods A and D implied the elimination each week of the piece of *Typha* leaf. Thereby, each week the unhatched eggs layed and fixed on the *Typha* were removed. However the results of Tables 1 and 2 show that the final density levels in the jars of methods A and D were not always lower than in jars B and C.

In spite of these methodological problems, the comparison of the 4 rearing methods A, B, C and D with the Mann-Whitney U test allows these methods to be arranged in the order of progressive efficiency for obtaining septifers. This order was A, B, D and C.

It can be inferred from the results of these experiments that the main factor which affected septum development was water quality. When the water was not renewed (methods C and D), it became heavily loaded with organic products of degradation (of animal and vegetable nature). In jars of method C, the oxygen content was low, whereas the accumulation of organic substances was very large. These conditions are similar to that found in nature when the mud is still covered by a thin layer of water (Richardot, 1972, 1976). In the laboratory as in the field, these conditions seem to be the most favorable for septum formation.

Further experiments are needed to show the exact role of the chemical parameters of the water, for example, the oxygen content.

TABLE 4. Experiment 4; accumulation of organic matter in the water (rearing method C).

	Time 0	week 1	week 2	week 3	week 4	week 5	week 6
Organic matter content mg 0_2/l	5	11	13	17	29	25	27
		12	13	22	25	27	35

The main outcome of the present experiments is that we have now a simple rearing method for obtaining septifers in the laboratory. We can obtain at will under laboratory conditions septum development and, later, any renewal of more favorable environment triggers off a resumption of growth (post-septifer form). Therefore, it is now possible to investigate all phases of the physiological mechanisms involved in this unusual estivation (only the submature individuals are able to develop a septum, thereby avoiding unfavorable environmental conditions). Furthermore, since results obtained previously (Richardot et al., 1972) provide evidence for a complete similarity in crystalline structure (aragonite) between shell and septum of *Ferrissia*, this mollusc is very suitable for the study of calcium metabolism and the mechanisms involved in shell formation (Richardot, 1976).

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ECOLOGICAL FACTORS INDUCING ESTIVATION IN THE FRESHWATER LIMPET *FERRISSIA WAUTIERI* (BASOMMATOPHORA: ANCYLIDAE). II. PHOTOPERIOD, LIGHT INTENSITY AND WATER TEMPERATURE

Monique Richardot

ABSTRACT

It has been shown previously that the septate form of estivation in *Ferrissia wautieri* is initiated by low oxygen content of the water and high organic matter content. The present study shows that photoperiod and water temperature play a conspicuous role in determining septum formation, whereas the effect of light intensity appears to be less significant. In laboratory populations, high percentages of septifers are obtained in "summer rearing conditions": a photoperiod of 16 hrs light and a high water temperature (25°-30°C).

INTRODUCTION

In a previous paper (Richardot, 1977), it was shown that the main factor initiating septum development is the chemical quality of the water. Observations and experiments carried out in the natural habitat of *Ferrissia* have indicated the positive role of high organic matter content and decreased oxygen (Richardot, 1976, 1977). When these conditions are experimentally obtained in the laboratory, the septum percentages in populations can rise to 75% or more. The present study was conducted to determine the role played by other ecological factors, such as photoperiod, light intensity and water temperature on determining septum development.

METHODS

In each experiment the limpets came from the same strain. Two rearing methods were set up. In the 1st method (C) 40 newly hatched juveniles were immersed in 250 ml of water with a piece of a *Typha* leaf in each 375 ml jar. Water and *Typha* were collected in the natural habitat. The jars were covered with a transparent plastic sheet; the water temperature was 25°C; the photoperiod was 16 hrs light, and the spatial variation in light intensity was 600-900 lux. Food (an equal part of the same *Typha* leaf in each jar) was distributed at weekly intervals. This rearing method, therefore, consisted of water progressively loaded with organic substances.

In the 2nd rearing method (E), the newly hatched juveniles were immersed in water previously loaded with organic substances. Six weeks before the start of the experiment several 375 ml jars, each with 250 ml of water and pieces of *Typha* leaves, were placed in conditions similar to the previous method, but without any limpets. After 6 weeks the organic matter content of the water was high (30-45 mg O_2/l) and the oxygen content was low (0-1 mg O_2/l). This water was used for the experiment. Five newly hatched juveniles were immersed in 15 ml of this water with a piece of a *Typha* leaf in each 45 ml glass jar. These smaller jars (covered with a transparent plastic sheet) were placed under conditions (photoperiod, light intensity and temperature) similar to that of method C. At weekly intervals equal parts of the same *Typha* leaf were distributed in the jars. The oldest pieces of leaves were removed, so that during the experimental period (except the 1st week) each jar contained 2 pieces of *Typha* leaf.

TABLE 1. Effect of photoperiod on initiating septum development. Comparison of 8 hours light and 16 hours light. Results after 4 weeks. Rearing method C. I, total number of individuals; E, total number of eggs; j, juveniles which were less than 1.29 mm long; s, submature individuals which were less than 2.58 mm long; m, mature individuals which were more than 2.58 mm long; S, number of septifers; %, septifer percentage.

Jar	I	E	No. of ancyloids j	s	m	S	No. of ancyloids s + m & S	%
Photoperiod: 8 hours light								
L1	37	18	3	28	5	1	34	2.9
L3	35	14	1	33	1		34	0
L5	39	2	2	36	1		37	0
L7	39		7	32			32	0
L9	40	5	7	33			33	0
L11	32	5	4	27		1	28	3.5
L13	31	50	5	24	2		26	0
L15	37	21	3	32	2		34	0
Photoperiod: 16 hours light								
L2	35	21	6	16	3	10	29	34.4
L4	36	3	5	22		9	31	29.0
L6	38		3	20	1	14	35	40.0
L8	35		5	23		7	30	23.3
L10	33	7	3	29	1		30	0
L12	35	18	6	22	2	5	29	18.5
L14	31	19	4	17	1	9	27	34.6
L16	38	1	2	28	1	7	36	20.0

Experiments carried out with method C allow a population to be observed when grown under ecological conditions which are degrading. This situation is similar to that of the natural habitat in summer (Richardot, 1976, 1977). The obvious advantage of method E is that in each jar there were only 5 limpets. Therefore, it was possible to follow the growth of each animal. Moreover, the experiment could be considered ended for each jar when the 5 limpets either had layed the 1st eggs or had developed a septum.

In the present study, experiments were conducted which consisted in rearing 2 series of limpets: one group according to method C or E (control); for the other (test) group, the rearing conditions were similar, except for one different factor – either photoperiod, light intensity or water temperature.

Septifer percentages obtained with method C were calculated with regard to the total number of living limpets which were 1.29 mm long or more (1.29 mm is the shell length of the smallest septifer

TABLE 2. Effect of photoperiod on initiating septum development. Comparison of 8 hours light and 16 hours light. Results after 6 weeks. Rearing method C. I, total number of individuals; E, total number of eggs; j, juveniles which were less than 1.29 mm long; s, submature individuals which were less than 2.58 mm long; m, mature individuals which were more than 2.58 mm long; S, number of septifers; %, septifer percentage.

Jar	I	E	No. of ancyloids j	s	m	S	No. of ancyloids s + m & S	%
Photoperiod: 8 hours light								
L1	91	201	55	25	8	3	36	8.3
L3	45	44	9	34	2		36	0
L5	49	26	11	33	4	1	38	2.6
L7	36	6	2	34			34	0
L9	46	7	11	33	2		35	0
L11	46	25	7	28	1	3	32	9.3
L13	55	55	26	24	5		29	0
L15	49	39	14	31	4		35	0
Photoperiod: 16 hours light								
L2	45	36	15	14	2	14	30	46.6
L4	34	8	2	12		20	22	62.5
L6	37	4	2	14	1	20	35	57.1
L8	34	14	1	14		19	33	57.5
L10	43	23	13	14	1	15	30	50.0
L12	47	27	17	13	2	15	30	50.0
L14	51	45	21	8	1	21	30	70.0
L16	44	7	12	8	2	22	32	68.7

obtained in the laboratory or collected in the natural habitat during 10 years). Thus, in the data obtained, all limpets (of the 1st and 2nd generations) which had reached or overtaken the period of septum development were taken into account.

The septifer percentages obtained were analysed with non-parametric tests (Siegel, 1956), i.e., the Mann-Whitney U test. Shell lengths were measured by means of an ocular micrometer.

EXPERIMENTS AND RESULTS

Photoperiod

A 1st series of experiments was performed to compare the results obtained with a summer

TABLE 3. Effect of photoperiod on initiating septum development. Comparison of 8 hours light and 16 hours light. Results after 10 weeks. Rearing method C. I, total number of individuals; E, total number of eggs; j, juveniles which were less than 1.29 mm long; s, submature individuals which were less than 2.58 mm long; m, mature individuals which were more than 2.58 mm long; S, number of septifers; %, septifer percentage.

Jar	I	E	No. of ancyloids j	s	m	S	No. of ancyloids s + m & S	%
Photoperiod: 8 hours light								
L1	90	125	55	23	8	4	35	11.4
L3	50	49	16	31	3		34	0
L5	64	11	26	32	5	1	38	2.6
L7	66	11	25	37	4		41	0
L11	56	19	14	38	1	3	42	7.1
L13	102	50	51	41	10		51	0
L15	76	72	36	28	8	4	40	10.0
Photoperiod: 16 hours light								
L2	108	148	68	13	6	21	40	52.5
L4	40	23	3	11		26	37	70.2
L6	58	64	22	11		25	36	69.4
L8	73	51	42	6		25	31	80.6
L12	55	51	13	23	2	17	42	40.4
L14	81	91	27	25	1	29	55	52.7
L16	107	114	60	12	5	30	47	63.8
Counter experiment: 8 hours light → 16 hours light								
L9	78	35	32	21	2	23	46	50.0

photoperiod (16 hrs light) and a winter photoperiod (8 hrs light). In a 2nd series of experiments one group of limpets was exposed to an intermediate photoperiod of 12 hrs light, and another group to a summer photoperiod (16 hrs light). All of these experiments were performed in the spring. The parents of the experimental animals were kept in summer conditions (25°C, 16 hrs light).

Comparison between 16 and 8 hour photoperiods

The 1st experiment was carried out with 640 *Ferrissia* distributed in 16 jars and reared according to method C. Eight jars were exposed to a winter photoperiod (8 hrs light). The

TABLE 4. Effect of photoperiod on initiating septum development. Comparison of 8 hours light (J) and 16 hours light (C). Rearing method E. I, number of individuals; Med, median size (mm); S, number of septifers.

	2nd week			3rd week			4th week			5th week			6th week			7th week		
Jar	I	Med	S	I	Med	S	I	Med	S	I	Med	S	I	Med	S	I	Med	S
J1	4	1.29		4	1.59		4	1.85		4	2.15		4	2.19		4	2.19	
J2	4	1.50		4	1.89		4	1.93		4	2.06		4	2.06		4	2.06	
J3	4	1.42		4	1.76		3	2.02		3	2.19		3	2.28		3	2.28	
J4	3	1.55		3	1.93		3	2.19		3	2.32		3	2.36		3	2.36	
J5	3	1.38		3	1.89		3	2.19		3	2.36		3	2.41		3	2.41	
J6	5	1.33		4	1.81		3	2.11		3	2.19		3	2.24		1	2.45	
J7	3	1.29		1	2.88		1	3.27		1	3.27		1	3.35				
J8	5	1.25		4	1.76		4	2.02		4	2.24		4	2.41		4	2.49	
C1	4	1.25		4	1.63	1	4	1.89	2	4	2.06	4	4	2.15	4	4	2.15	4
C2	4	1.38		4	1.76	2	4	1.98	2	4	2.15	4	4	2.19	4			
C3	5	1.55		5	1.68	2	4	1.89	3	4	2.19	3	4	2.24	3			
C4	4	1.76	1	4	1.93	2	4	2.11	2	4	2.24	3	4	2.24	3	4	2.19	3
C5	4	1.76		4	2.06	1	4	2.19	4									
C6	2	1.85		2	2.24	1	2	2.41	2									

2nd (70 limpets) and the 3rd (75 limpets) experiments were carried out according to culture method E.

The tables 1, 2 and 3 show data of the 1st experiment after 4, 6 and 10 weeks. The total number of animals 4 weeks after the start of the experiment was about the same in the jars exposed to a summer photoperiod as in the jars exposed to a winter photoperiod. The mortality was significant but similar in both cases. The 2nd generation subjects were probably not numerous. In the "winter jars" only 2 septifers occurred, whereas in the "summer jars" 61 were found. Two weeks later, the increase in density of the populations in the 16 jars implied an emergence of a 2nd generation. The difference between the septifer percentages obtained in the "winter jars" and in the "summer jars" was highly significant ($U = 0$, significant for $P = 0.01$) if we consider only the limpets larger than 1.29 mm in shell length. After 10 weeks, only 14 jars were of concern. Some animals from the 2nd generation were larger than 1.29 mm in shell length. There was an increase in the density of septifers and the difference between the "summer jars" and the "winter jars" remained significant ($U = 0$).

A control experiment was performed with "winter jar" L9. At the end of the 6th week this jar with 48 juvenile ancyloids was exposed to a summer photoperiod. Four weeks later 23 septifers were present in this jar. The septifer percentage (50%) was similar to that previously obtained in the other "summer jars".

Seven weeks after the start of the 2nd experiment (culture method E) the total numbers of surviving subjects were similar (22) in the 8 "winter jars" and in the 6 "summer jars"

TABLE 5. Effect of photoperiod on initiating septum development. Comparison of 8 hours light (J) and 16 hours light (C). Rearing method E. I, number of individuals; Med, median size (mm); S, number of septifers.

	2nd week			3rd week			4th week			5th week			6th week		
Jar	I	Med	S	I	Med	S	I	Med	S	I	Med	S	I	Med	S
J8	3	2.11		3	2.15		3	2.36		3	2.41		3	2.41	
J9	5	1.46		5	1.59		5	1.68		5	1.81		5	1.93	
J10	4	1.63		4	1.89		4	2.24		4	2.28		4	2.36	
J11	4	1.89		4	2.02	1	4	2.24	1	4	2.32	1	4	2.41	1
J12	5	1.50		4	1.55		4	1.76		4	2.02		4	2.24	
J13	5	1.89		5	2.06		5	2.15		5	2.28		5	2.32	
J14	5	1.20		5	1.50		5	1.81		5	1.93		5	1.98	
J15*	6	1.98		6	2.11		6	2.15		6	2.24		6	2.28	
C7	5	1.81		5	1.98	3	5	2.06	4	5	2.11	5	5	2.11	5
C8	5	1.59	1	5	1.89	2	5	2.15	3	5	2.24	3	5	2.24	3
C9	5	1.63		5	1.85	3	5	2.06	3	5	2.15	5	5	2.15	5
C10	5	1.76	1	5	1.89	3	5	1.98	5	5	1.98	5			
C11	4	1.89		4	2.11	1	4	2.24	2	4	2.32	3	4	2.32	3
C12	5	1.59		5	1.72	1	5	1.89	3	5	1.98	4	5	2.06	5
C13	5	1.72		5	2.06	1	5	2.24	2	5	2.24	4	5	2.24	4

*6 limpets, instead of 5, were placed in this jar.

(Table 4); therefore the mortality was slightly higher in the "winter jars". No septifers occurred in the "winter jars", whereas in the "summer jars" 86.9% of the animals were septate.

In experiment 3 (Table 5), the mortality was similar in the 2 series of jars after 6 weeks. In the "winter jars", 1 limpet had a septum, whereas in the "summer jars" 73.5% of the limpets were septate.

Comparison between the 16 and 12 hour photoperiods

Experiment 4 was performed with culture method C. Eighty limpets were placed in 2 jars. One jar was exposed to a photoperiod of 12 hrs light and the other to a summer photoperiod (16 hrs light). After 6 weeks (Table 6) only 4.3% of the surviving animals larger than 1.29 mm were septate in the test jars, but 58.3% were septate in the control jars. Ten weeks later the percentages were 4.1% and 74.5% respectively.

Experiment 5 was carried out according to culture method E and included 150 limpets,

TABLE 6. Effect of photoperiod on initiating septum development. Comparison of 12 hours light (E) and 16 hours light (C). Rearing method C. I, total number of individuals; E, total number of eggs; j, juveniles which were less than 1.29 mm long; s, submature individuals which were less than 2.58 mm long; m, mature individuals which were more than 2.58 mm long; S, number of septifers; %, septifer percentage.

Jar	I	E	No. of ancyloids j	s	m	S	No. of ancyloids s + m & S	%
6th week								
E	62	28	3	41	3	2	46	4.3
C	96	35	48	16	4	28	48	58.3
10th week								
E	134	146	86	43	3	2	48	4.1
C	97	95	38	11	4	44	59	74.5

75 of which were exposed to a photoperiod of 12 hrs light (test) and 75 (control) to a summer photoperiod. After 2 weeks (Table 7), the limpets remaining were about equal in number in both the test jars (65) and the control jars (64). At the end of the experiment no septifer had been found in the test jars, whereas in the control jars 73.4% of the limpets had a septum.

Light intensity

A 1st series of experiments was performed to compare the results obtained in 2 groups of 160 limpets reared according to method C and exposed to different light intensities. One group (test) was exposed to a spatial variation in light intensity from 1600 to 2000 lux, the other group (control) to light intensity from 400 to 900 lux. In a 2nd series of experiments one group of 50 *Ferrissia* (control) were exposed to a spatial variation in light intensity from 400 to 900 lux, and another group of 50 *Ferrissia* (test) were exposed to a low light intensity (3-10 lux). The limpets were reared according to method E.

The results of the 1st series of experiments are presented in Table 8. Six weeks after the start of the experiment the septum percentages were clearly low in the test jars (2000 lux). They were significantly different from the percentages obtained in the control jars (900 lux) ($U = 0$). Ten weeks later the number of septifers increased in the 2 groups (test and control) and some limpets of the 2nd generation were estivating. The difference between the septifer percentages in the test jars and in the control jars were no longer significant ($U = 4$).

Table 9 shows the data obtained in the 2nd series of experiments (900 lux and 10 lux). Two weeks after the start of the experiment the mortality was higher in the test jars (35 surviving limpets) than in the control jars (42 surviving limpets). At the end of the experiments the septifer percentages were almost similar in the test jars (91%) and in the control jars (97%).

TABLE 7. Effect of photoperiod on initiating septum development. Comparison of 12 hours light (E) and 16 hours light (C). Rearing method E. I, number of individuals; Med, median size (mm); S, number of septifers.

	2nd week			3rd week			4th week			5th week		
Jar	I	Med	S	I	Med	S	I	Med	S	I	Med	S
E1	5	1.68		5	2.13		5	2.27		5	2.33	
E2	5	1.46		5	1.99		5	2.03		5	2.12	
E3	5	1.55		5	2.00		5	2.09		5	2.26	
E4	4	1.44		4	1.94		4	2.07		4	2.22	
E5	5	1.46		5	2.13		5	2.47		5	2.54	
E6	4	1.26		4	1.87		4	2.28		4	2.45	
E7	1	1.93		1	2.79							
E8	4	1.30		4	1.77		4	1.86		4	1.94	
E9	3	1.40		3	1.87		3	2.04		3	2.21	
E10	5	1.29		5	1.78		5	2.02		5	2.18	
E11	5	1.57		5	2.06		5	2.17		5	2.34	
E12	5	1.46		5	1.80		5	1.94		5	2.16	
E13	4	1.54		3	2.15		3	2.16		3	2.33	
E14	5	1.57		5	1.93		5	1.90		5	1.91	
E15	5	1.37		5	1.68		5	1.83		5	2.01	
C1	4	1.40		3	1.77		3	2.45		3	2.67	1
C2	5	1.48		5	1.98		5	2.21	2	5	2.31	4
C3	5	1.32		5	1.82		5	2.04		5	2.17	1
C4	4	1.24		4	1.77	1	4	2.08	2	4	2.18	4
C5	4	1.25		4	1.70		4	2.04	3	4	2.12	3
C6	3	1.46		3	1.91	1	3	2.24	1	3	2.50	2
C7	4	1.43		4	1.94		4	2.15	4	4	2.27	4
C8	3	1.53		3	2.20		3	2.34		3	2.49	1
C9	5	1.18		5	1.52		5	1.73		5	1.86	3
C10	4	1.56		4	2.03	1	4	2.11	4	4	2.23	4
C11	4	1.31		4	1.89		4	2.04	2	4	2.06	2
C12	5	1.38		5	1.85		5	2.11	1	5	2.19	3
C13	4	1.64		4	1.98	1	4	2.02	4	4	2.12	4
C14	5	1.31		5	1.63		5	1.83	1	5	1.99	4
C15	5	1.68		5	1.84		5	1.94	3	5	1.97	3

TABLE 7. (Cont.)

6th week			7th week			8th week			9th week			10th week		
I	Med	S	I	Med	S	I	Med	S	I	Med	S	I	Med	S
5	2.42		3	2.21		3	2.46		3	2.62		3	2.90	
5	2.16		5	2.20		5	2.31		5	2.34		5	2.54	
5	2.29		5	2.35		5	2.41		5	2.56		5	2.85	
4	2.29		4	2.30		4	2.38		4	2.38		4	2.43	
5	2.54		5	2.63		5	2.79		4	2.74		4	2.85	
4	2.52		4	2.64		4	2.72		4	3.07		4	3.07	
4	2.13		4	2.28		4	2.42		4	2.69		4	2.85	
3	2.38		3	2.54		3	2.73		3	2.86		3	2.98	
5	2.37		5	2.40										
5	2.53		5	2.53		5	2.58		5	2.60		5	2.76	
5	2.19		4	2.21		4	2.33		3	2.67		3	2.81	
3	2.47		3	2.59		3	2.80		3	3.05		2	3.01	
5	1.98		4	1.91		4	1.97		4	2.08		4	2.24	
5	2.17		4	2.37		4	2.54		4	2.69		4	3.01	
3	2.67	1												
5	2.38	4												
5	2.21	1	5	2.25	2	5	2.25	3	5	2.25	3			
3	2.17	3												
4	2.13	3	4	2.17	3									
3	2.59	2												
4	2.33	4												
3	2.51	1	3	2.64	1									
5	1.86	3	5	1.88	3									
4	2.08	3	4	2.08	3									
5	2.23	3												
4	2.15	4												
5	2.01	4	5	2.07	4									
5	2.00	4	5	2.15	5									

TABLE 8. Effect of light intensity on initiating septum development. Comparison of 2000 lux and 900 lux. Rearing method C. L, light intensity (lux); I, total number of individuals; E, total number of eggs; j, juveniles which were less than 1.29 mm long; s, submature individuals which were less than 2.58 mm long; m, mature individuals which were more than 2.58 mm long; S, number of septifers; %, septifer percentage.

Jar	L	I	E	No. of ancyloids			S	No. of ancyloids s + m & S	%
				j	s	m			
6th week									
N1	2000	58	48	24	23	8	3	34	8.8
N3	2000	52	11	13	34	5		39	0
N5	2000	118	40	79	31	6	2	39	5.1
N7	2000	50	6	12	30	6	2	38	5.2
N2	900	62	32	22	25	7	8	40	20.0
N4	900	58	69	19	24	5	10	39	25.6
N6	900	53	40	20	29		4	33	12.1
N8	900	128	16	89	8	8	23	39	58.9
10th week									
N1	2000	163	47	118	14	9	22	45	48.8
N3	2000	179	38	161	7	6	5	18	27.7
N5	2000	130	12	96	20	10	4	34	11.7
N7	2000	98	49	69	16	6	7	29	24.1
N2	900	167	73	122	18	11	17	46	36.9
N4	900	171	166	121	19	9	22	50	44.0
N6	900	245	91	207	17	10	11	38	28.9
N8	900	175	42	118	23	10	24	57	42.1

Temperature of the water

Two series of experiments were performed to compare the effect of 3 temperatures: 18°, 25° and 30°C.

In the 1st series, 50 limpets (control) were distributed in 10 jars which were kept at 25°C, and 50 limpets were kept at 18°C (culture method E). In the 2nd series of experiments, 50 limpets (control) were kept at 25°C and 50 limpets at 30°C (culture method E).

In the 1st series (25°, 18°) the septifer percentages were calculated with regard to the number of living individuals recorded 2 weeks after the start of the experiment (on account of the slowing down of the growth rate at 18°C); the septifer percentages were calculated

TABLE 9. Effect of light intensity on initiating septum development. Comparison of 10 lux (R) and 900 lux (S). Rearing method E. I, number of individuals; Med, median size (mm); S, number of septifers.

	2nd week			3rd week			4th week			5th week			6th week			7th week		
Jar	I	Med	S	I	Med	S	I	Med	S	I	Med	S	I	Med	S	I	Med	S
R1	4	1.46		4	1.84	3	4	1.92	4	4	1.95	4	4	1.95	4			
R2	3	1.31		3	1.79	2	3	1.96	3	3	1.98	3	3	1.98	3			
R3	2	1.65		2	1.93	1	1	1.98	1	1	1.98	1	1	1.98	1			
R4	4	1.72	2	4	1.90	3	4	1.94	3	4	2.00	4	4	2.00	4			
R5	3	2.04	2	3	2.06	3												
R6	4	1.75	2	4	1.91	3	4	1.96	4	4	1.99	4						
R7	5	1.64		5	1.79	5	5	1.82	5	5	1.88	5						
R8	4	1.47		4	1.81	2	4	1.87	3	4	1.87	3						
R9	3	1.70		3	1.95	2	3	2.02	3	3	2.10	3						
R10	3	1.13		3	1.46	2	3	1.54	2	3	1.54	2						
S1	4	2.04	1	4	2.09	4	4	2.09	4	4	2.13	4						
S2	4	1.59		4	1.88	3	4	1.98	4	4	2.04	4	4	2.04	4			
S3	4	1.61		4	1.90	3	4	2.03	4	4	2.03	4	4	2.03	4			
S4	4	1.79	1	4	1.93	4	4	2.00	4									
S5	5	1.70	2	5	1.81	3	5	1.89	3	5	1.97	5	5	1.97	5	5	1.99	5
S6	4	1.50		4	1.79	2	4	1.95	4	4	2.00	4						
S7	5	1.82	3	5	1.94	5	5	1.99	5	5	1.99	5	5	1.99	5			
S8	5	1.79	1	5	2.07	5	5	2.09	5	5	2.17	5						
S9	2	1.87		2	2.51	1	2	2.64	1	2	2.64	1						
S10	5	1.30		5	1.47	1	5	1.57	2	5	1.61	2	5	1.82	3	5	1.94	5

one week after the start of the experiment in the 2nd series (25°, 30°). The results (Table 10) show that septum formation was markedly inhibited by the low temperature. The septifer percentages were significantly different from those obtained at 25°C (U = 18, significant for P = 0.05). On the other hand, the septifer percentages were not significantly different for the limpets kept at 25°C and 30°C (U = 50) (Table 11).

DISCUSSION

The results provided by this study show the effects of some ecological factors on initiating estivation in *Ferrissia*. The data of the 1st experiments lead us to assume that the photoperiod plays an important role in septum formation and in determining estivation.

TABLE 10. Effect of temperature on initiating septum development. Comparison of 25°C (C) and 18°C (F). Rearing method E. I, number of individuals; Med, median size (mm); S, number of septifers; R, septifer ratio.

	2nd week			3rd week			4th week			5th week			6th week		
Jar	I	Med	S	I	Med	S	I	Med	S	I	Med	S	I	Med	S
C1	5	1.55		5	1.76	1	5	1.98	4	5	2.02	4	5	2.06	4
C2	4	1.29		4	1.85	2	4	1.93	3	4	2.24	3	4	2.28	3
C3	5	1.42		5	1.55	2	4	1.93	3	4	2.02	4	4	2.06	4
C4	4	1.72		4	2.02	3	4	2.15	4	4	2.15	4			
C5	5	1.85		5	2.02	3	5	2.11	3	5	2.19	3	4	2.24	3
C6	4	1.76		4	2.06	3	4	2.19	3	4	2.28	3			
C7	5	1.59		5	1.81	2	5	1.98	5	5	2.02	5	5	2.06	5
C8	5	1.55		4	1.89	2	4	2.11	3	4	2.15	3	4	2.19	3
C9	3	1.50		3	1.89	2	3	2.19	2	3	2.54	2			
C10	2	1.89		2	2.06	2	2	2.15	2	2	2.15	2			
F1	5	1.03		5	1.42		5	1.81		5	2.06		4	2.45	
F2	4	1.29		4	1.76		4	1.98	2	4	2.19	4	4	2.24	4
F3	5	1.29		5	1.63		5	1.85		5	1.93	1	5	2.02	1
F4	5	1.07		4	1.81		4	2.24	2	4	2.28	3	4	2.28	3
F5	5	1.07		5	1.72		5	1.98	1	5	2.19	1	5	2.28	1
F6	5	1.20		5	1.59		5	1.89	1	5	1.98	1	5	2.15	2
F7	5	1.16		5	1.55		5	1.81		5	2.02		5	2.06	1
F8	4	1.55		4	2.02		4	2.11	3	4	2.24	4	4	2.19	4
F9	3	0.90													
F10	2	0.95		2	1.38		2	1.85		2	2.19		2	2.67	

The duration of daylight must be longer than 12 hours. However, the presence of some septifers in populations exposed to a winter photoperiod suggests that the circadian rhythm does not act alone but in association with the 25°C temperature; such a high temperature does not occur in winter in the natural habitat of *Ferrissia*. So in the present experiments the association of 2 ecological factors have been tested: photoperiod and temperature. The association of a long daylight period and a high temperature (25°C) is obviously efficient in obtaining septifers in the laboratory.

The results of the experiments concerning the effect of light intensity suggest that low light intensity may play a role in septum formation and initiating estivation in *Ferrissia*. In the 1st series of experiments the results are clear after 6 weeks. Later (10 weeks) the influence of this ecological factor decreased in intensity. Further experiments are needed to show if the effect of light intensity is then supplanted by the influence of the increase

TABLE 10. (Cont.)

7th week			8th week			9th week			10th week			
I	Med	S	I	Med	S	I	Med	S	I	Med	S	R
												4/5
												3/4
												4/5
												4/4
												3/5
												3/4
												5/5
												3/5
												2/3
												2/2
4	2.49		4	2.49		4	2.62		4	2.62		0/5
4	2.28	4										4/4
5	2.06	1	5	2.11	1	5	2.15	1	5	2.24	1	1/5
4	2.32	3										3/5
5	2.45	1	5	2.28	1	5	2.36	1				1/5
5	2.19	2	5	2.19	2	5	2.28	2	5	2.28	2	2/5
5	2.15	2	5	2.19	2	5	2.24	2	5	2.24	2	2/5
												4/4
2	2.92											0/2

in organic matter and the decrease in oxygen content of the water.

It can be inferred from the 1st experiments concerning temperature that high temperatures are obviously favorable for septum formation. As has been observed for ancyloids (Richardot & Wautier, 1966) in the laboratory, these temperatures have a direct effect on the growth rate of the limpets, but they probably have only an indirect effect on septum development – by inducing an increase in the organic matter content of the water and a decrease in the oxygen content.

Taken together, these observations are in agreement with results obtained in the natural habitat of *Ferrissia wautieri* (Richardot, 1976, 1977). Evidence is now presented to show that the chemical quality of the water cannot act separately. It has to be associated at least with a summer photoperiod and high temperatures.

So, as it has been observed in other molluscs, estivation intervenes when the individual is subjected to a conjunction of different ecological factors (Fischer, 1950; D. Bonavita,

TABLE 11. Effect of temperature on initiating septum development. Comparison of 25°C (A) and 30°C (P). Rearing method E. I, number of individuals; Med, median size (mm); S, number of septifers; R, septifer ratio.

	1st week			2nd week			3rd week			4th week		
Jar	I	Med	S	I	Med	S	I	Med	S	I	Med	S
A1	5	1.29		5	1.68		4	1.76	2	4	1.85	2
A2	4	1.33		4	1.93		4	2.06		4	2.06	2
A3	5	1.20		5	1.59		5	1.81	1	5	1.93	3
A4	5	1.33		5	1.93		5	2.02	4	5	2.02	4
A5	3	1.25		3	1.76		3	2.11	2	3	2.15	3
A6	4	1.38		4	1.76		4	2.11	4	4	2.15	4
A7	5	1.25		5	1.89		5	2.15	4	5	2.15	4
A8	5	1.16		4	1.50		4	1.85	1	4	1.89	3
A9	5	1.42		5	1.76		5	1.89		5	2.02	1
A10	4	1.55		4	2.11		4	2.19	4	4	2.19	4
P1	4	1.81		4	2.11	1	4	2.19	2	4	2.19	2
P2	5	1.50		5	1.93		5	2.11	3	5	2.19	3
P3	5	1.59		5	1.98	1	5	2.02	4	5	2.02	4
P4	5	1.59		4	1.98	1	4	2.15	3	4	2.19	3
P5	5	1.55		5	1.89	4	5	2.02	5	5	2.11	5
P6	4	1.50		4	1.85	2	4	1.89	3	4	2.02	3
P7	5	1.59		5	1.72	4	5	1.93	4	5	1.98	5
P8	5	1.42		5	1.63		5	1.76	1	5	1.85	3
P9	5	1.55		5	1.93		5	2.15	3	5	2.19	3
P10	5	1.46		5	1.85	1	5	1.93	5	5	1.93	5

1964; A. Bonavita, 1965; Abeloos, 1965; Pomeroy, 1968; Sturrock, 1970; Din, 1971; Gainer, 1972).

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TABLE 11. (Cont.)

5th week			6th week			7th week			8th week			
I	Med	S	I	Med	S	I	Med	S	I	Med	S	R
4	2.02	3	4	2.11	3							3/5
4	2.15	2	4	2.15	2	4	2.19	2				2/4
5	2.02	3	5	2.11	4	5	2.28	4	4	2.24	4	4/5
5	2.11	5	5	2.11	5	5	2.11	5				5/5
3	2.19	3	3	2.19	3							3/3
4	2.19	4										4/4
												4/5
4	2.06	3	4	2.11	3							3/5
4	2.19	1	4	2.36	3	4	2.36	3				3/5
4	2.24	4										4/4
4	2.28	2	4	2.36	2							2/4
												3/5
												4/5
4	2.24	3										3/5
												5/5
4	2.11	4	4	2.11	4							4/4
5	2.02	5										5/5
5	1.89	4	5	2.11	4							4/5
5	2.24	3										3/5
5	1.98	5										5/5

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TOLERANCE OF *BIOMPHALARIA GLABRATA* EMBRYOS TO CONTINUOUS THERMAL STRESS[1]

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ABSTRACT

Nearly 10,000 embryos of *Biomphalaria glabrata* were continuously subjected to temperatures ranging from 25-39°C. Temperatures below 35°C appeared to have no adverse effect on the development of pre-gastrula and post-gastrula snails. However, at higher temperatures, snails developed abnormalities early. At 35°C, approximately 83 hours and 100 hours of exposure were necessary to prevent hatching in pre- and post-gastrula embryos, respectively.

INTRODUCTION

To understand more fully the habits of aquatic organisms, it is necessary to know their thermal limitations. Van der Schalie & Berry (1973a,b) found the range of temperature tolerance of adults of 7 species of aquatic snails to be quite narrow. Other studies with molluscan embryos, primarily with those of *Lymnaea stagnalis* Linnaeus, have shown that developing freshwater snails are sensitive to heat shock (see Raven, 1966; Verdonk & de Groot, 1970). However, little work has been done with gastropod embryos that were continually stressed with heat. Two significant reasons for studying the effects of temperature on molluscs are (1) to determine the potential effect from thermal waste water on them, and (2) to obtain data for possible use of heated water as a non-chemical control of snails transmitting schistosomiasis.

Earlier heat studies with *Biomphalaria glabrata* (Say) have been concerned with the hatched snail (Michelson, 1961; Chernin, 1967; Mousa & El-Hassan, 1972; Sturrock & Sturrock, 1972). Previously, studies on the effects of thermal stress on embryos of *B. glabrata* have been limited. El-Hassan (1974) established minimum and maximum thermal thresholds and incubation periods at various temperatures for *B. alexandrina* (Ehrenberg), but did no work with different embryological stages and heat-induced abnormalities. Similar, but less detailed, data were presented by Sturrock (1966) for *B. pfeifferi* (Krauss). Camey & Verdonk (1970) did an extensive investigation of the normal development of *B. glabrata.* Our study investigated: (1) viability of pre-gastrula embryos at temperatures ranging from 25-39°C, (2) viability of post-gastrula embryos at temperatures ranging from 33-39°C, (3) the duration of heat stress at 35°C required to prohibit hatching in embryos of *B. glabrata*, and (4) heat-induced abnormalities.

MATERIALS AND METHODS

Egg masses of *Biomphalaria glabrata* (Puerto Rican strain) were collected daily with feather-weight forceps or razor blades and transferred to plastic baskets suspended in 8-gallon (30.28 liters) aquaria in a flow system designed by van der Schalie & Berry (1973a). Windows of nylon monofilament screen cloth (Tetko, Inc.) with 295 μ openings allowed aerated tapwater to flow through the baskets to the developing embryos. Small pockets of the same screen were used to isolate egg masses collected during

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a single day. Eggs were incubated in 9 aquaria at temperatures ranging from 25-39°C and kept in alternating periods (12 hrs) of light and darkness. Temperature, pH and dissolved oxygen for each tank were checked periodically.

The initial stage of development and the number of eggs per mass were recorded prior to each experiment. During incubation, each egg case was inspected daily for development. Once hatching began, egg masses were removed from the temperature controlled aquaria and hatching was allowed to continue at room temperature. Number hatched, dead, and abnormal were recorded. To delineate cell boundaries, some embryos were stained with silver nitrate according to the procedure developed by Verdonk (1965). In one experiment, pre- and post-gastrula embryos were stressed at 35°C for varying lengths of time. After this exposure, they were returned to room conditions and subsequently examined for normal or abnormal development.

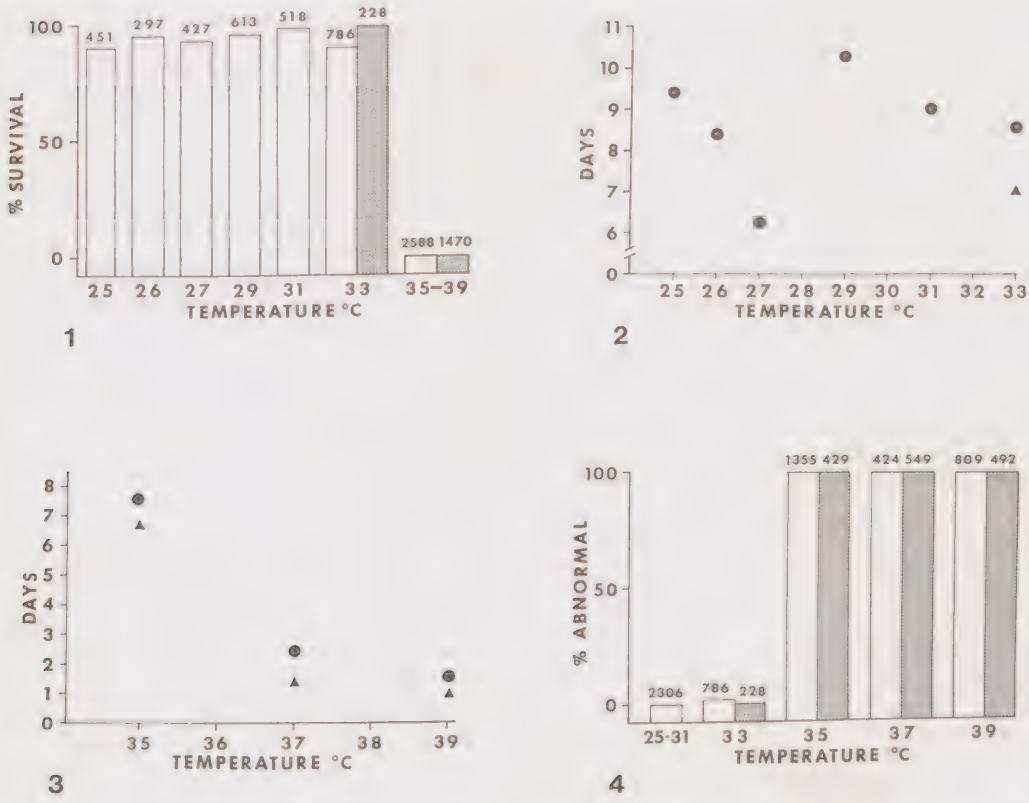
For this study pre-gastrula embryos included only uncleaved, 2-celled or 4-celled stages at the start of an experiment. Post-gastrula stages included those embryos with well defined albumen cells and early head vesicles.

RESULTS

Survival and hatching of *Biomphalaria glabrata* embryos did not appear to be adversely affected by continuous exposure to temperatures ranging from 25-33°C. Data shown in Fig. 1 indicate that the majority (94.7%) of pre-gastrula embryos subjected to these temperatures hatched. However, those exposed to higher temperatures died before they could emerge. The incubation period of both the pre- and post-gastrula embryos varied with the temperature (Fig. 2). At temperatures of 25, 26, and 27°C, the hatching times of pre-gastrula embryos were 9.3, 8.5, and 6.4 days respectively. But at 29°C, a dramatic change was observed. Pre-gastrula snails exposed to that temperature did not hatch until they had incubated for more than 10 days. At 31 and 33°C, the incubation period decreased to approximately 9 days. In contrast, post-gastrula embryos hatched after 7 days when exposed to 33°C. At 33°C, a few pre-gastrula embryos (2%) showed abnormal development, while post-gastrula embryos showed no abnormal development.

Embryos of *Biomphalaria glabrata* are not able to tolerate temperatures above 34°C. Fig. 3 illustrates the average number of days pre- and post-gastrula embryos survived at temperatures ranging between 35-39°C. Although snails subjected to 35°C did survive for nearly a week, none hatched. Warmer temperatures (37-39°C) usually killed both stages of embryos by the end of the 2nd day. At 35-39°C, all embryos developed abnormalities. In a separate experiment, pre- and post-gastrula embryos were stressed at 35°C for varying lengths of time. Some 83 hrs of stress at this temperature were necessary to induce abnormalities so that no pre-gastrula embryos hatched. Post-gastrula embryos at the same temperature required 100 hrs of exposure to prevent hatching.

The developmental abnormalities produced by continuous exposure to temperatures beyond the normal range were of the same types as those produced by heat shock; however, at temperatures above 35°C the percentage of abnormal embryos may approach 95% (Fig. 4), while heat shock usually resulted in fewer than 20% abnormal embryos. The majority of abnormal embryos produced resulted from abnormal gastrulation or exogastrulation. Figs. 7 and 9 indicate the cell pattern of the anterior and posterior halves of an exogastrulated embryo produced by continuous treatment at 35°C. The yolk remained uncovered by ectoderm, the apical plate cells were abnormal in number, shape and distribution, and the cephalic plate areas were not clearly delineated. The posterior ectoderm (Fig. 9) remained as undivided large cells in contrast to the normal small-celled ectoderm produced in control embryos. Fig. 10 shows the maximum developmental potential of a partially exogastrulated embryo. The ectoderm differentiates only into large and small cells with none of the specialized areas apparent. The endoderm may be vesicular of large



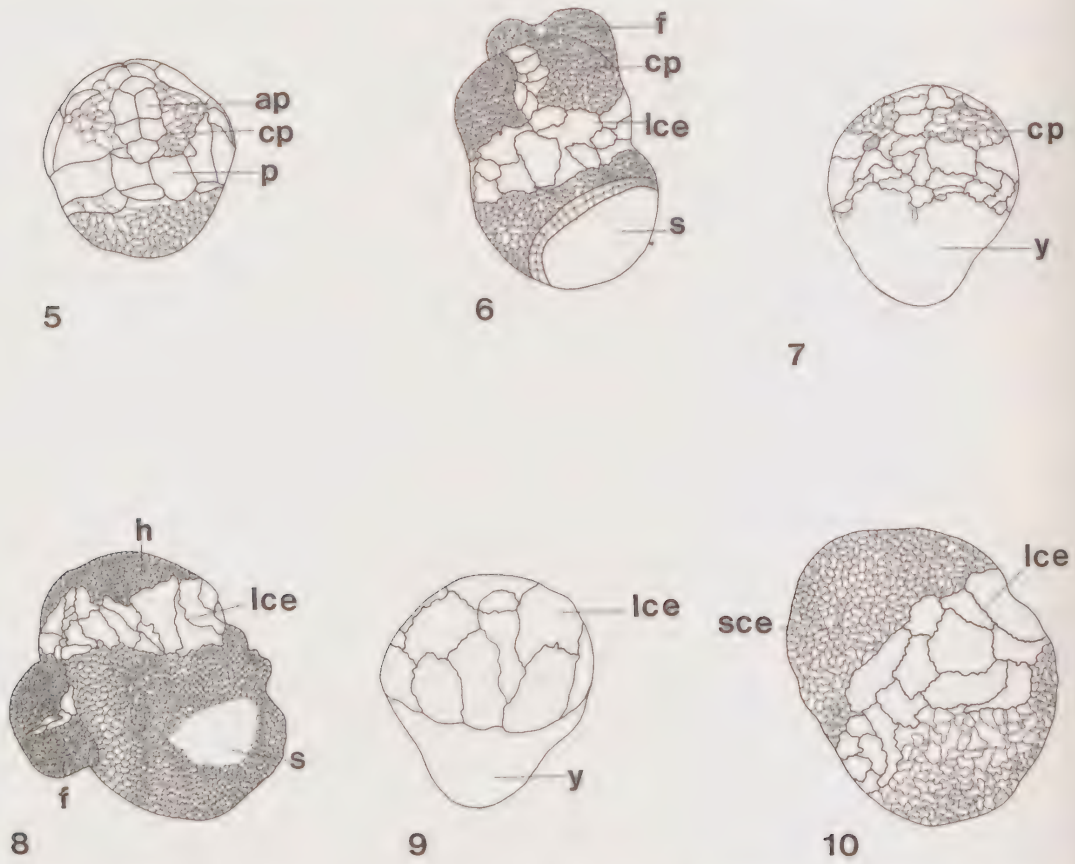
FIGS. 1-4. Effects of temperature on *Biomphalaria glabrata*. FIG. 1. Percentage of survival to hatching of pre-gastrula (unshaded) and post-gastrula (shaded) embryos exposed to continuous temperatures of 25-39°C. FIG. 2. Mean incubation period of pre-gastrula (circles) and post-gastrula (triangles) embryos subjected to temperatures ranging from 25-33°C. FIG. 3. Longevity of pre-gastrula (circles) and post-gastrula (triangles) embryos exposed to temperatures of 35-39°C. FIG. 4. Percentage of abnormal pre-gastrula (unshaded) and post-gastrula (shaded) embryos resulting from exposure to various temperatures (25-39°C). Numbers at top of column represent embryos tested.

and small cells. Mesenchyme cells, ganglia and nerves were present but poorly organized. Exogastrulated embryos usually failed to undergo further morphogenesis under continuous heat treatment and died relatively unchanged.

In embryos which do gastrulate, there tended to be many head abnormalities. Fig. 6 shows an embryo lacking eye anlagen, while Fig. 8 shows a heat stressed embryo which appeared normal while living but after staining showed fewer and larger cells in the prototroch than is normal; an asymmetry of the cephalic plates and the number of apical plate cells were fewer than normal. Abnormal embryos, even those with minor head defects, have not been observed to hatch after continuous heat treatment.

DISCUSSION

Increased temperatures have been used extensively to study sensitive developmental periods in molluscan embryos (see Geilenkirchen, 1966; Verdonk & de Groot, 1970). Heat shocks up to ½-hr were used, rather than continuous exposure to high temperatures. Geilenkirchen studied the periods of early development in detail and found that the cleavage



FIGS. 5-10. Effects of high temperature (35°C) on embryos of *Biomphalaria glabrata*. All embryos were reared at 35°C from the 2-cell stage until fixed and stained with silver nitrate to indicate the cell boundaries. ap, apical plate; cp, cephalic plate; f, foot; h, head region; lce, large-celled ectoderm; p, prototroch; s, shell; sce, small-celled ectoderm; y, yolk. FIG. 5. Embryo at 24 hrs. The number of cells in the apical plate is reduced, the cephalic plates are asymmetrical and poorly delimited, and the prototroch has fewer cells than normal which are larger in size and abnormal in position. FIG. 6. Embryo at 72 hrs. This embryo is similar to the controls of 5-6 days, except that it lacks eyes. FIG. 7. Exogastrulated embryo at 24 hrs. The cell pattern is irregular, with possible cephalic plate differentiation. The yolk remained exposed. FIG. 8. Embryo of 72 hrs. The majority of the head is absent; no apical plate is formed; the foot is extruded laterally, and an area of ectodermal specialization may represent the shell gland. FIG. 9. Exogastrulated embryo of 24 hrs. This is the opposite side of the embryo shown in Fig. 7. Only large-celled ectoderm is differentiated. FIG. 10. Exogastrulated embryo at 72 hrs. Only large- and small-celled ectoderm are differentiated externally.

period was most sensitive to heat shock. Verdonk & de Groot studied the production of head abnormalities and found that they were related to treatment at the stages when the 1st quartet of micromeres were dividing, either for the 1st or 2nd time. They observed that gastrulation could be arrested directly by heat shock, and that the embryos were arrested at that stage rather than later. The maximum number of exogastrulae were produced by heat treatment in early development, i.e., up until 3 hrs after the 3rd cleavage. Raven (1952) analysed the developmental capacity of exogastrulae and found that they could differentiate small- and large-celled endoderm, small- and large-celled ectoderm,

the stomodeum, larval kidney and mesenchyme. We found defects among embryos continually treated at 35°C similar to those found in embryos treated with heat shock. We failed to find any defects not previously described in heat-shocked embryos; however, the percentage of defects was greatly increased by continuous exposure to high temperature. The inability of embryos to hatch was closely correlated to observed abnormalities. Continual treatment of embryos at temperatures less than 35°C had no effect other than reducing the incubation period with increasing temperature. Continual treatment at temperatures greater than 35°C quickly resulted in death so that no further development occurred. Post-gastrula embryos showed fewer extreme abnormalities; a longer treatment in high temperature was necessary to kill them.

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THIRTEEN NEW SPECIES OF LAND SNAILS FROM THE SOUTHEASTERN UNITED STATES WITH NOTES ON OTHER SPECIES

Leslie Hubricht

ABSTRACT

Thirteen new species of land snails are described from the southeastern U.S.A. These are *Stenotrema morosum*, fossil, Bakers Bluff Cave, Tennessee (Polygyridae); *Glyphyalinia ocoae*, near Parksville, Tennessee; *Paravitrea alethia*, near Blair, Tennessee; *P. bellona*, near Earling, West Virginia; *P. ceres*, Buckeye, West Virginia; *P. dentilla*, near Damascus, Virginia; *P. septadens*, near Bee, Virginia; *P. subtilis*, near Lafayette, Tennessee; *P. ternaria*, near Ernestville, Tennessee; *P. tiara*, near Guntersville, Alabama; *P. varidens*, Roan Mt., North Carolina (Zonitidae); *Helicodiscus bonamicus*, near Beechertown, North Carolina (Endodontidae); *Carychium riparium*, near Brandenburg, Kentucky (Carychiidae).

Stenotrema morosum new species
Figs. 1-3

Description. Shell small, subglobose with convexly conoidal spire, imperforate, whorls 5, strongly convex, periphery rounded; embryonic whorls with numerous, fine, radially-elongate pustules, later whorls with numerous growth lines and hair scars; aperture narrow, basal lip with adnate outer edge, inner edge callused; lip notch deep and narrow, being more than twice as deep as wide, the callus margin extending outward and downward to below the base of the lip; interdenticular sinus deeply rounded; tooth in the outer arc of the lip moderately developed; parietal tooth well developed, high, sinuous, the outer end curving into the interdenticular sinus, butress well developed.

Height 4.4 mm, diameter 6.5 mm, whorls 5. Holotype.

Distribution. *Tennessee:* Sullivan Co.: fossil, in Bakers Bluff Cave, Halls Mill (Type Locality) (Carnegie Museum Expedition, coll.), Holotype 187059 and Paratypes 187060, Field Museum of Natural History (FMNH), other Paratypes 45652, collection of the author.

Remarks. *Stenotrema morosum* is most closely related to *S. pilula* (Pilsbry), differing in the deeper and narrower lip notch and the very heavy development of the callus around it. This callus curves downward to below the base of the shell. In this character it differs from any other species of *Stenotrema*. It is known only from a Pleistocene to Recent deposit within a cave.

Microceramus pontificus (Gould 1848)

Microceramus pontificus (Gould). Pilsbry, 1946: 109.
Microceramus floridanus (Pilsbry). Pilsbry, 1946: 110.

There is no constant difference in size, shape, ribbing, or crenulation of the shells which would warrant the recognition of more than one species of *Microceramus* in Florida. *M. texanus* (Pilsbry) from the Edwards Plateau in Texas has more numerous but less elevated ribs and appears distinct. Also, it occurs in an area which may get quite cold in the winter, while *M. pontificus* is restricted to tropical Florida.

FIGS. 1-3. *Stenotrema morosum* Hubricht, Holotype. FIGS. 4-6. *Glyphyalinia ocoae* Hubricht, Holotype. [Drawings (Figs. 1-33, 41) by Elizabeth A. Liebman, courtesy of Field Museum of Natural History.]

Glyphyalinia ocoae new species
Figs. 4-6, 34

Description. Shell small, strongly depressed, shining, translucent, pale yellow-orange; whorls 4.5 to 5, rapidly increasing, sutures shallow; periphery and base rounded, umbilicus small, contained about 24 times in the diameter of the shell, sealed with hardened slime, or may be rimate; 1st whorl smooth, later whorls with regular sub-equidistant, impressed radial lines which extend into the umbilicus, and numerous fine spiral striae between the radial lines; aperture rather large, ovate-lunate, lip thin, simple.

Animal pale blueish-gray. Penis club-shaped, with the retractor muscle attached to the distal end; epiphalis with 2 distinct sections, attached below the distal end of the penis, proximal section somewhat convoluted, distal section sausage-shaped with a distinct caecum where it joins the proximal section.

Height 1.9 mm, diameter 4.8 mm, aperture height 1.5 mm, aperture width 2.2 mm, umbilicus diameter 0.2 mm, 4.5 whorls. Holotype.

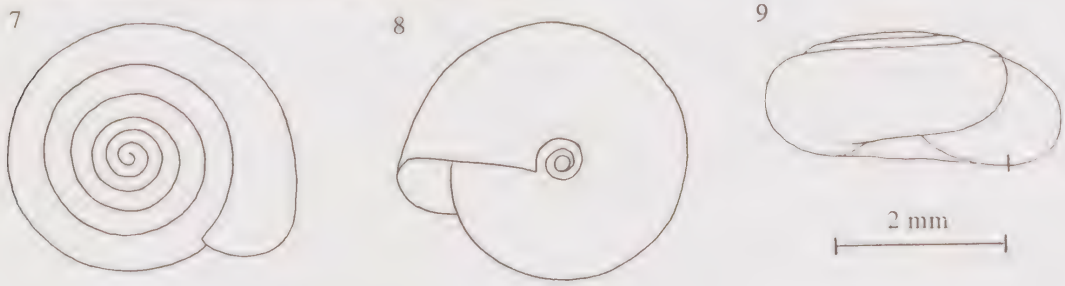
Distribution. *Tennessee:* Polk Co.: ravine, 6 miles east of Parksville (Type Locality), Holotype 187070 and Paratypes 187071 FMNH, other Paratypes 45209, collection of the author; Sugarloaf Mountain, near Parksville; ravine, 2 miles east of Ocoee; base of hill, 4.6 miles east of Parksville; ravine, 3 miles southwest of Archville; near mouth of Goforth Creek; Thunder Rock Recreation area, near Ocoee Dam no. 3; Hiwassee River bluff, southwest of Wetmore.

Remarks. *Glyphyalinia ocoae* has been confused with *G. indentata* (Say) but is quite distinct by its anatomy. The shell differs in being smaller and in being darker colored. Its true affinities are obscure as there is no other species with the caecum on the epiphalis as in this species.

Paravitrea septadens new species
Figs. 7-9

Description. Shell small, pale brownish, subhyaline; spire very low, nearly discoidal, with shallow sutures; whorls 6, slowly increasing, last quarter whorl slightly expanded in mature shells; periphery somewhat flattened, base somewhat flattened; umbilicus deep, well-like, contained about 7 times in the diameter of the shell; aperture narrowly lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous irregularly spaced impressed growth-lines, which are much weaker below; within the last whorl occur 1 or 2 radial lamellae (which may be absent in mature shells).

Height 1.6 mm, diameter 3.4 mm, aperture height 1.2 mm, aperture width 1.6 mm, umbilicus diameter 0.6 mm, 6.0 whorls. Holotype.



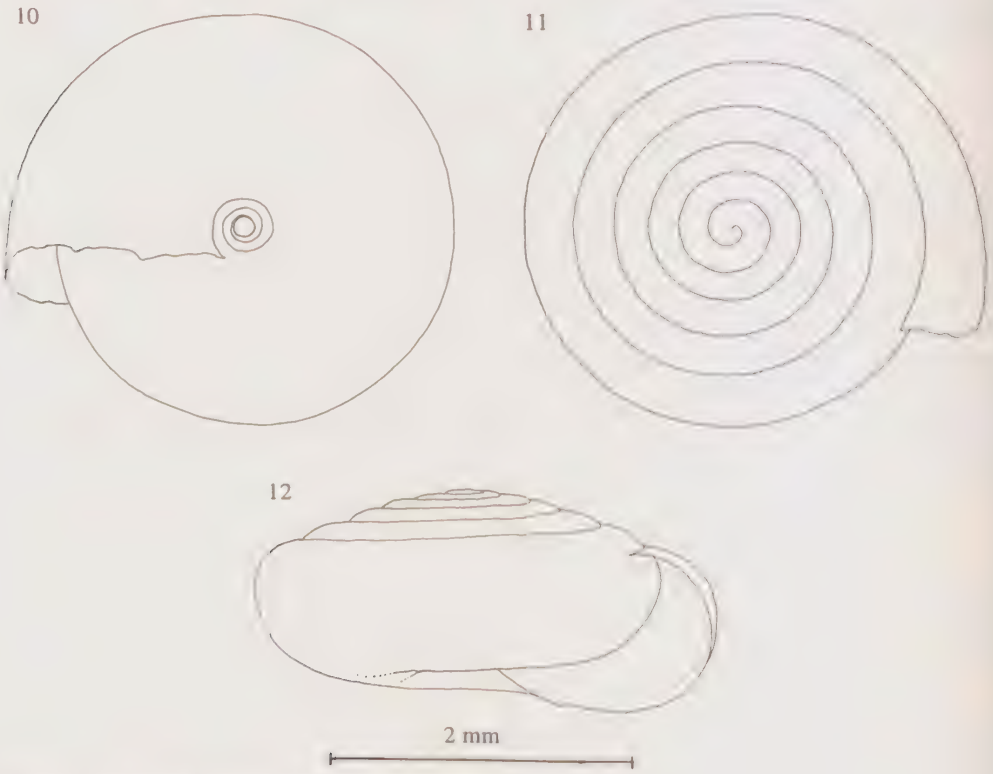
FIGS. 7-9. *Paravitrea septadens* Hubricht, Holotype.

Distribution. *Virginia:* Dickenson Co.: ravine, 1.6 miles west-northwest of Bee (Type Locality), Holotype 171660 and Paratype 171661 FMNH, other Paratypes 44932, collection of the author; Grassy Creek Gorge, Breaks Interstate Park; ravine, 2.5 miles northeast of Haysi; ravine, 2 miles southeast of Birchleaf; ravine, 2.8 miles southeast of Birchleaf. Buchanan Co: base of hill, 2.4 miles west of Stacey; base of hill, 3.2 miles southeast of Oakwood.

Remarks. *Paravitrea septadens* differs from *P. multidentata* (Binney) in having a more rounded periphery, a smaller umbilicus, and fewer and weaker growth lines. The lamellae are radial rather than oblique as in form *lamellata* H. B. Baker. It is most closely related to *P. amicalola* Hubricht, differing in being smaller and in having the lamellae persisting until the shell is adult or nearly so.

Paravitrea subtilis new species
Figs. 10-12

Description. Shell small, pale reddish-brown, subhyaline, shining; spire very low conoid, with shallow sutures; whorls 6 to 6.5, slowly increasing, expanding near the aperture; whorls angulate when young, becoming rounded at maturity, periphery high on the whorl; umbilicus deep, contained about 7 times in the diameter of the shell at maturity, but up to about twice that in immature shells; first 2 whorls smooth, later whorls with numerous closely but somewhat irregularly spaced impressed growth-lines, becoming more widely spaced and irregular on the last whorl, weaker below the periphery; 1 or 2 radial rows of 4 to 6 teeth in the last whorl (coalesced in some specimens to form a lamella).



FIGS. 10-12. *Paravitrea subtilis* Hubricht, Holotype.

Height 1.4 mm, diameter 2.9 mm, aperture height 1.1 mm, aperture width 1.2 mm, umbilicus diameter 0.4 mm, 6.3 whorls. Holotype.

Distribution. *Tennessee:* Macon Co.: ravine, 5 miles southeast of Lafayette (Type Locality), Holotype 187068, Paratypes 187069, FMNH, other Paratypes 41651, collection of the author. Fentress Co.: 1200 ft., mountainside, 2 miles west of Jamestown. *Kentucky:* Rockcastle Co.: near Climax Cave, near Climax. Bell Co.: Pine Mountain Gap, 0.5 mile south of Pineville. Harlan Co.: 2000 ft., north side of Pine Mountain, 2 miles southeast of Bledsoe. Perry Co.: wooded hillside, 0.5 mile south of Fusonia; wooded hillside, 2.3 miles southwest of Slemp. *Virginia:* Wise Co.: ravine, 2400 ft., 3.4 miles west of Inman.

Remarks. *Paravitrea subtilis* differs from *P. multidentata* (Binney) in having more widely and more irregularly spaced growth-lines. In the shape of the shell it resembles *P. variabilis* H. B. Baker, but it lacks the spiral sculpture of that species. *P. amicalola* Hubricht is a larger shell and the teeth are found only in immature shells.

Paravitrea dentilla new species
Figs. 13-15

Description. Shell small, very pale brownish, subhyaline, shining; spire very low conoidal, sutures distinct; whorls 7.5 to 8, slowly increasing, last whorl not expanded behind the lip; periphery rounded, base rounded; umbilicus deep and well-like, contained about 5.5 times in the diameter of the shell; aperture lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous irregularly spaced, impressed growth lines, distinct above but becoming obsolete below; immature shells with 1 or more radial rows of 5 or 6 small teeth within the last whorl, the teeth are set close together the bases usually touching, the adults are toothless.

Height 3.5 mm, diameter 6.8 mm, aperture height 2.5 mm, aperture width 2.9 mm, umbilicus diameter 1.2 mm, 8 whorls. Holotype.

Distribution. *Virginia:* Washington Co.: base of mountain 1 mile south of Damascus (Type Locality), Holotype 171656, Paratype 171657, FMNH, other Paratypes 10650, collection of the author; bluff along Laurel Creek, Damascus.

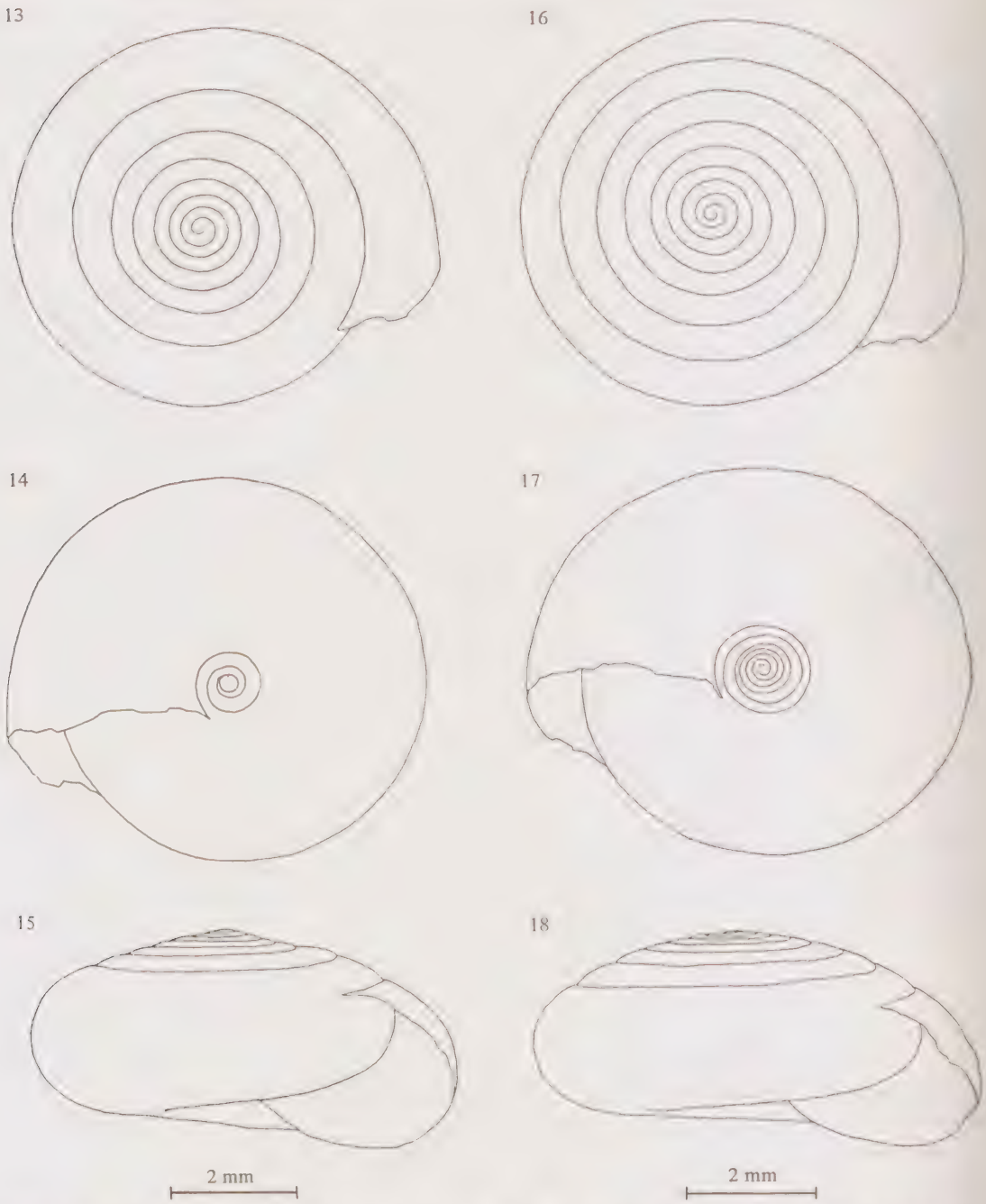
Remarks. *Paravitrea dentilla* is most closely related to *P. varidens* Hubricht, differing in having more and smaller teeth. Immature shells might be confused with those of *P. multidentata* (Binney), but the sculpture is different.

Paravitrea ternaria new species
Figs. 16-18

Description. Shell small, pale brownish, subhyaline, shining; spire very low dome-shaped, sutures well marked; whorls 8.5, slowly increasing, last whorl slightly expanded behind the lip; periphery rounded, base rounded; umbilicus deep and well-like, rather large, contained about 5 times in the diameter of the shell; aperture narrowly lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous, irregularly spaced, impressed growth lines, distinct above but subobsolete below; within the last whorl there are usually 2 or 3 radial rows of 3 rather large teeth, which are present at all stages of growth.

Height 3.4 mm, diameter 6.8 mm, aperture height 2.2 mm, aperture width 1.4 mm, umbilicus diameter 1.4 mm, 8.5 whorls. Holotype.

Distribution. *Tennessee:* Unicoi Co.: ravine, 0.5 mile northeast of Ernestville (Type Locality), Holotype 171668, and Paratypes 171669, FMNH, other Paratypes 45076, collection



FIGS. 13-15, *Paravitrea dentilla* Hubricht, Holotype. FIGS. 16-18, *Paravitrea ternaria* Hubricht, Holotype.

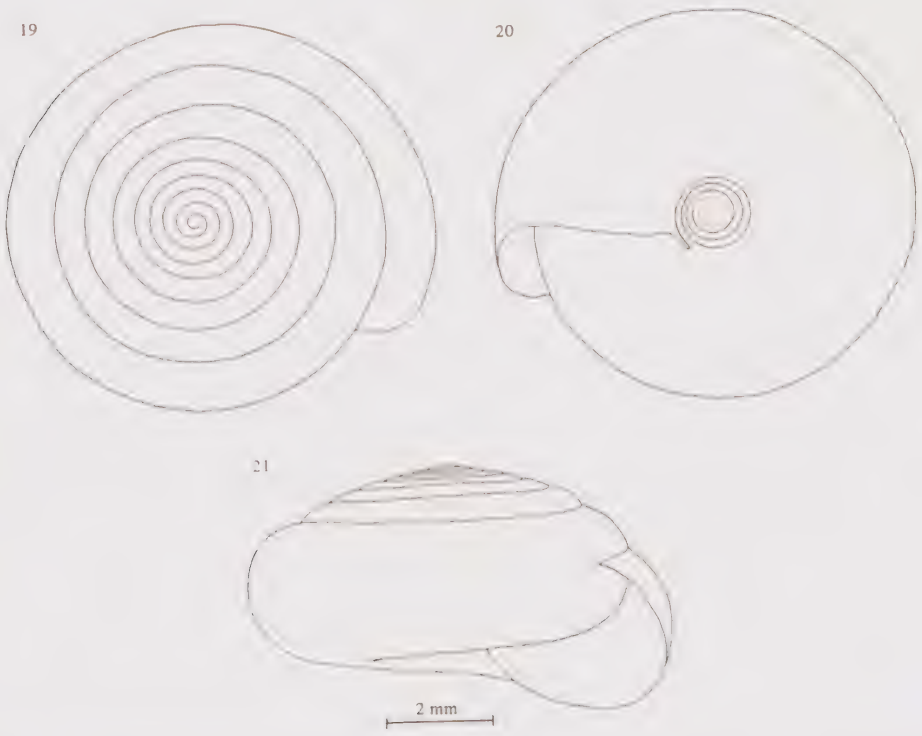
of the author; ravine, 3700 ft., 5.2 miles south of Flag Pond.

Remarks. *Paravitrea ternaria* is most closely related to *P. tridens* Pilsbry, differing in being larger, with a larger umbilicus, and with radial rows of 3 teeth present at all stages of growth. The animal is dark gray while the animal of *P. tridens* is nearly white.

Paravitrea varidens new species
Figs. 19-21

Description. Shell small, pale brownish, subhyaline, shining; spire low dome-shaped, sutures distinct; whorls 8.5 to 9, slowly increasing, last whorl slightly expanded behind the lip; periphery rounded, base rounded, excavated around the umbilicus; umbilicus deep and well-like, contained about 5 times in the diameter of the shell; aperture lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous irregularly spaced, impressed growth lines, distinct above but becoming obsolete below; adults toothless; immature shells with 2 or 3 radial rows of 3 or 4 rather large teeth within the last whorl (these teeth are sometimes fused to form a radial lamella).

Height 4.6 mm, diameter 7.6 mm, aperture height 2.9 mm, aperture width 3.4 mm, umbilicus diameter 1.5 mm, 9 whorls. Holotype.



FIGS. 19-21, *Paravitrea varidens* Hubricht, Holotype.

Distribution. *North Carolina:* Mitchell Co.: 6250 ft., summit of Roan Mountain (Type Locality), Holotype 171664, Paratype 171665, FMNH, other Paratypes 36513, collection of the author. Yancey Co.: wooded hillside, 1 mile northwest of Celo. *Tennessee*: Carter Co.: 4000 ft., north side of Roan Mountain, 2.5 miles south of Burbank; woods, 0.8 mile north of Burbank.

Remarks. *Paravitrea varidens* has been confused with *P. andrewsae* (Binney) of the same region. The latter has five teeth in each row which are present in adults, and the umbilicus is smaller. It is probably more closely related to *P. ternaria* Hubricht, differing in frequently having 4 teeth in a row, and in having them present only in immature shells.

Paravitrea tiara new species
Figs. 22-24, 42

Description. Shell small, pale brownish, subhyaline, shining; spire low conoidal, sutures shallow; whorls 7.5, slowly increasing, last whorl slightly expanded behind the lip; periphery rounded, base rounded; umbilicus deep and well-like, contained about 6 times in the diameter of the shell; aperture lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous, irregularly spaced, impressed growth lines, distinct above but becoming obsolete below; teeth are absent at all stages of growth.

Animal with gray foot, head and mantle; penis club-shaped, retractor muscle and epiphalis terminal; epiphalis about as long as the penis with a small caecum near its distal end.

Height 3.4 mm, diameter 6.0 mm, aperture height 2.3 mm, aperture width 2.9 mm, umbilicus diameter 0.9 mm, 7.5 whorls. Holotype.

Distribution. *Alabama:* Marshall Co.: wooded hillside, 1.3 miles north of Guntersville (Type Locality), Holotype 171663, Paratypes 171662, FMNH, other Paratypes 44645, collection of the author.

Remarks. *Paravitrea tiara* is most closely related to *P. capsella* (Gould), differing in having an elevated, toothless shell. Anatomically it differs in having the penial retractor and epiphalis terminal, and in having a more distinct caecum at its distal end. Anatomically it most closely resembles *P. tridens* Pilsbry, but is probably not closely related to that species.

Paravitrea alethia new species
Figs. 25-27, 43

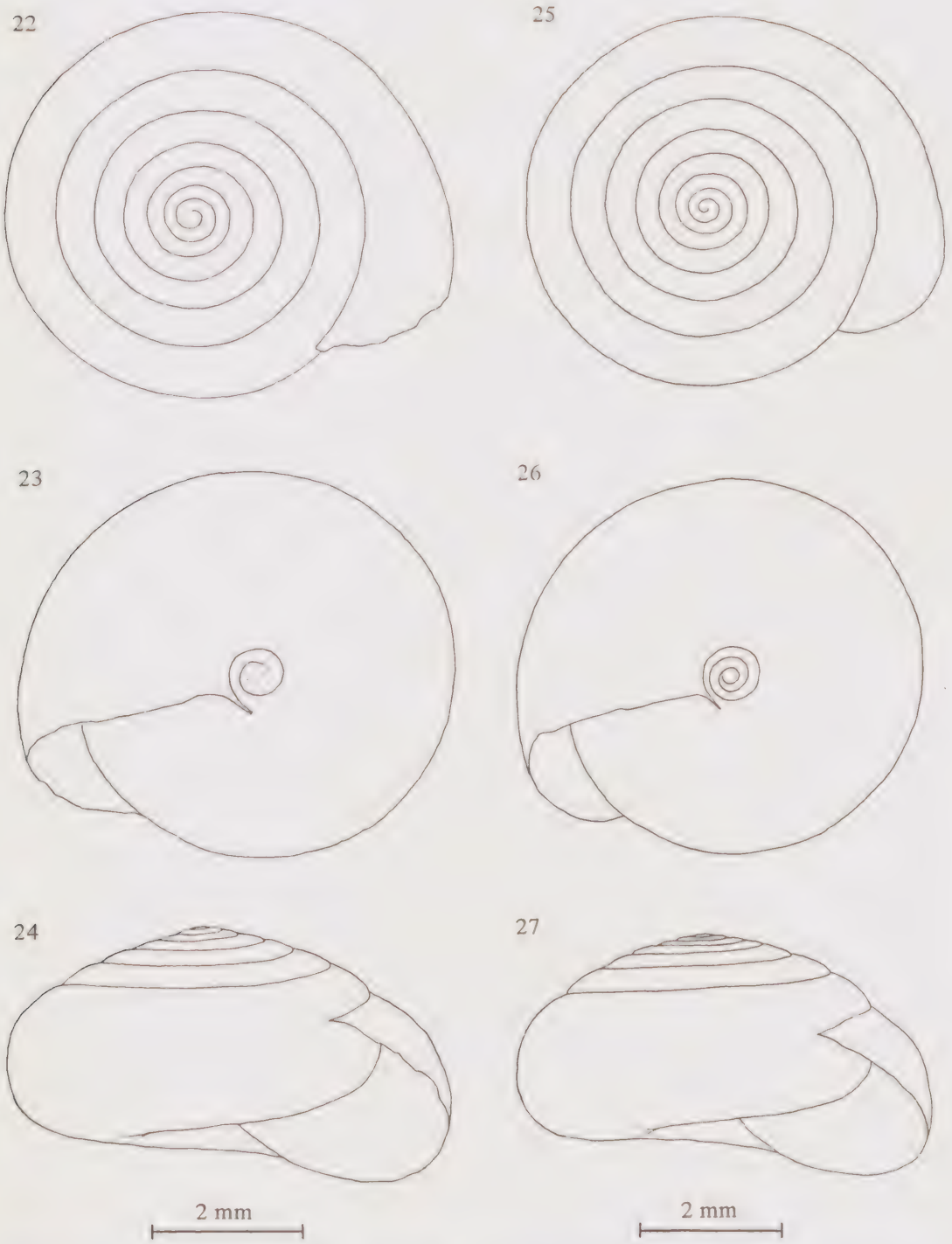
Description. Shell small, pale brownish, subhyaline, shining; spire low dome-shaped, sutures shallow; whorls 6.5 to 7, slowly increasing, last whorl expanded behind the lip; periphery rounded, somewhat deflected behind the lip, base rounded, somewhat excavated around the umbilicus; umbilicus deep and well-like, contained about 6 times in the diameter of the shell; aperture lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous, irregularly spaced, impressed growth lines, distinct above but becoming obsolete below; teeth are absent at all stages of growth.

Animal with gray foot, head and mantle; penis club-shaped, epiphalis about as long as the penis, without a caecum, attached below the tip of the penis; opposite the attachment of the epiphalis is a rather long appendix, about 1/2 as long as the penis, retractor muscle attached to the distal end of the appendix.

Height 3.4 mm, diameter 5.9 mm, aperture height 1.9 mm, aperture width 2.2 mm, umbilicus diameter 0.9 mm, 6.9 whorls. Holotype.

Distribution. *Tennessee:* Roane Co.: wooded hillside, 2.4 miles southwest of Blair (Type Locality), Holotype 171666, Paratypes 171667, FMNH, other Paratypes 27385, collection of the author.

Remarks. The shell of *Paravitrea alethia* is not really distinguishable from that of *P. tiara* Hubricht, but the 2 species are quite distinct anatomically. The presence of a very long appendix on the penis to which the retractor muscle is attached will distinguish *P. alethia* from any species for which the anatomy is known, except for *P. ceres* Hubricht. *P. capsella* (Gould), as this species has been understood in the past, is a complex of species differing anatomically but with very similar shells.



FIGS. 22-24, *Paravitrea tiara* Hubricht, Holotype. FIGS. 25-27, *Paravitrea alethia* Hubricht, Holotype.

Paravitrea bellona new species
Figs. 28-30, 35

Description. Shell small, pale brownish above, subhyaline, shining; spire very low convex-conoidal, sutures shallow; whorls 6.5 to 7, slowly increasing, not noticeably expanded behind lip; periphery rounded, base rounded; umbilicus deep and well-like, contained about 5 times in the diameter of the shell; aperture lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous, irregularly spaced, impressed growth lines, distinct above but becoming obsolete below; pairs of teeth are present in immature shells of less than 5 whorls but are absent in adults.

Animal with bluish-gray foot, head and mantle; penis club-shaped, retractor muscle and epiphalis terminal; epiphalis a little longer than the penis, its distal end slightly enlarged but without a caecum; about 1/3 of the proximal end of the epiphalis is attached to the penis.

Height 2.1 mm, diameter 5.8 mm, aperture height 2.2 mm, aperture width 2.4 mm, umbilicus diameter 1.3 mm, 7 whorls. Holotype.

Distribution. *West Virginia:* Logan Co.: wooded hillside, 0.5 mile northwest of Earling (Type Locality), Holotype 187066, Paratypes 187067, FMNH, other Paratypes 46090, collection of the author; Horsepen Mountain, 4.5 miles south of Sarah Ann. Mingo Co.: Guyandot River bluff, opposite Justice; river bluff, 0.6 mile south of Tamcliff; river bluff, 0.8 mile south of Gilbert. Boone Co.: ravine, 2.7 miles south of Greenview.

Remarks. Anatomically *Paravitrea bellona* appears to be most closely related to *P. tiara* Hubricht, differing in the absence of a caecum on the epiphalis. The shell differs in having paired teeth in immature shells.

Paravitrea ceres new species
Figs. 31-33, 36

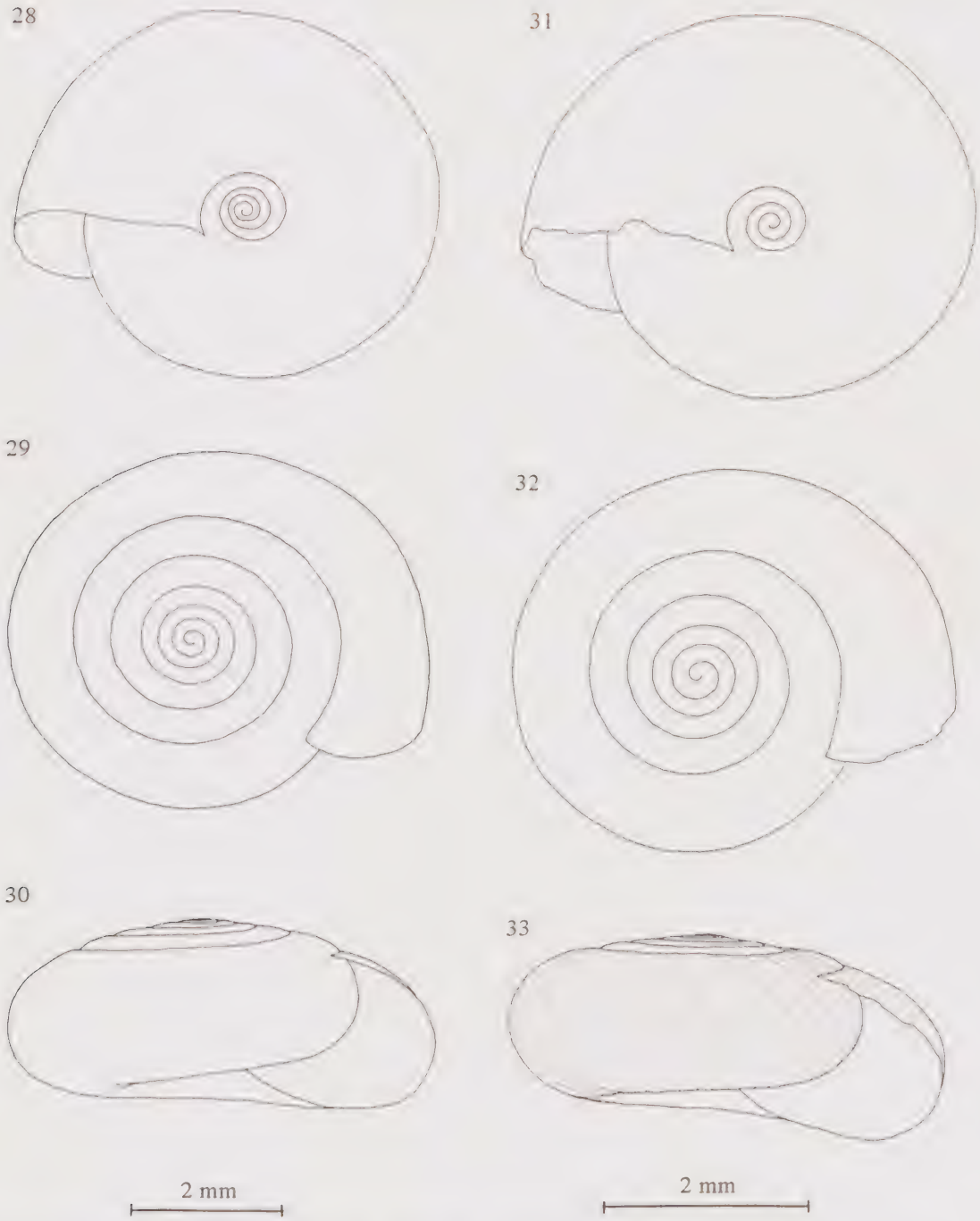
Description. Shell small, pale brownish, subhyaline, shining; spire very low, almost discoidal, sutures shallow; whorls 6, slowly increasing, last whorl a little expanded behind the lip; periphery rounded, base rounded; umbilicus deep and well-like, contained about 5 times in the diameter of the shell; aperture lunate, a little wider than high, lip thin, simple; nuclear whorl smooth, later whorls sculptured with numerous, irregularly spaced, impressed growth lines, distinct above but becoming obsolete below; adults toothless.

Animal with bluish-gray foot, head and mantle; penis slender, epiphalis about as long as the penis, without a caecum, attached at the tip of the penis, and to the side of the penis for nearly 1/2 of its length; below the summit of the penis is a distinct appendix, a little longer than the diameter of the penis; retractor muscle attached to the distal end of the appendix.

Height 2.0 mm, diameter 4.3 mm, aperture height 1.6 mm, aperture width 2.0 mm, umbilicus diameter 0.8 mm, 6 whorls. Holotype.

Distribution. *West Virginia:* Pocahontas Co: wooded hillside, Buckeye (Type Locality). Holotype 187062, Paratypes 187063, FMNH, other Paratypes 45975, collection of the author.

Remarks. *Paravitrea ceres,* by the presence of a lateral appendix to the penis, appears to be related to *P. alethia* Hubricht, but the appendix is much shorter than in that species. The shell differs in being smaller and more depressed. There are no specimens with less than 5 whorls in the type lot, so that it cannot be determined whether or not the immature shells are dentate.



FIGS. 28-30, *Paravitrea bellona* Hubricht, Holotype. FIGS. 31-33, *Paravitrea ceres* Hubricht, Holotype.

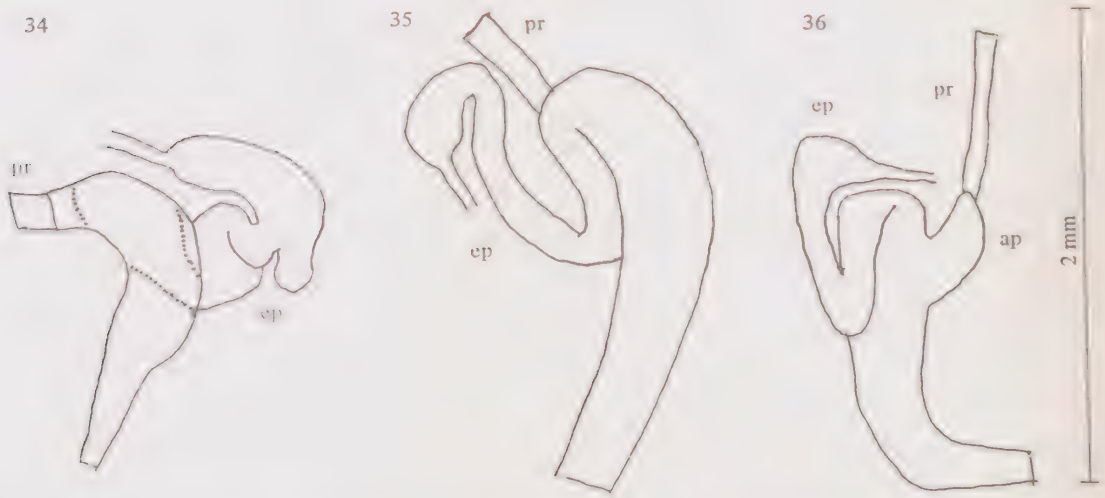


FIG. 34, *Glyphyalinia ocoae* Hubricht, penis and accessories. FIG. 35, *Paravitrea bellona* Hubricht, penis and accessories. FIG. 36, *Paravitrea ceres* Hubricht, penis and accessories. ap = appendix, ep = epiphalis, pr = penial retractor. [Drawings (Figs. 34-36, 42, 43) by the author.]

Hawaiia ? neomexicana (Cockerell & Pilsbry 1900)

Hawaiia minuscula neomexicana (Cockerell & Pilsbry). Pilsbry, 1946: 424.

This species differs from *Hawaiia minuscula* (Binney) in that the shell is rich golden-yellow rather than milky-white, has microscopic spiral striae, and the umbilicus is more open. It is found at higher elevations in the mountains of west Texas and New Mexico. It is doubtful that it belongs in the genus *Hawaiia*, but its affinities cannot be determined until the animal has been dissected.

Helicodiscus alachuana (Dall 1885)

Hawaiia minuscula alachuana (Dall). Pilsbry, 1946: 424.
Helicodiscus jacksoni Hubricht. Hubricht, 1962: 106.

Helicodiscus jacksoni is a synonym of what has been known as *Hawaiia minuscula alachuana*, which I believe to be a *Helicodiscus*. The shell of *He. alachuana* differs from *Ha. minuscula* in having smaller caliber whorls and a larger umbilicus and is usually smaller with the same number of whorls. The shell of *Ha. minuscula* sometimes shows narrow, opaque rings in the shell where the lip was thickened during a rest period. I have never seen these in *He. alachuana*. *Ha. minuscula* is a species of bare ground, usually found in grassy places, roadsides and along railroads, but is also found in floodplain woods. *He. alachuana* is usually found in leaf litter in woods, but in one case I found them together under old ties along a railroad. The animal of *He. alachuana* sometimes shows an orange margin to the mantle, which is characteristic of *Helicodiscus*.

Helicodiscus bonamicus new species
Figs. 37-40

Description. Shell small, discoidal, spire depressed, dull, opaque brownish-gray; umbilicus wide and shallow, contained about twice in the diameter of the shell; whorls 5, very slowly increasing in size, the last whorl deflected downward behind the aperture; aperture lunate, and oblique to the axis of the shell, lip slightly thickened, simple; sutures deeply and regularly impressed; whorls with numerous spiral lirae, 3 to 5 of which bear long deciduous hair-like processes; there is usually a pair of small tubercles well within the aperture.

Height 1.4 mm, diameter 4.2 mm, aperture height 1.1 mm, aperture width 1.1 mm, umbilicus diameter 2.3 mm, 5 whorls. Holotype.

FIGS. 37-40, *Helicodiscus bonamicus* Hubricht, Holotype. [Scanning Electron Microscope photographs (Figs. 37-40) by Dr. Alan Solem, courtesy of Field Museum of Natural History.]

Distribution. *North Carolina:* Macon-Swain Co. line: base of mountain, Nantahala Gorge, near Handpole Creek, 0.4 mile north of Beechertown (Type Locality) (Glenn A. Goodfriend; Leslie Hubricht, colls), Holotype 187064, Paratypes 171321 and 187065, FMNH, other Paratypes 45824, collection of the author.

Remarks. *Helicodiscus bonamicus* is most closely related to *H. fimbriatus* Wetherby, differing in its longer, larger, more distinct and deciduous hairs, in its shallower umbilicus, and in the reduced internal teeth.

Catinella vagans (Pilsbry 1900)

Quickella vagans (Pilsbry). Pilsbry, 1946: 843.

Catinella vagans is a valid species, distinct from *C. vermeta* (Say). Pilsbry's figs. 456A and 456B are of *C. vagans* and show that the penis and appendix are of about the same size. Fig. 456C is of *C. vermeta* from Lake Waccamaw, North Carolina, and shows the inflated appendix characteristic of that species. The shell of *C. vagans* has a much shorter spire than that of *C. vermeta*. *C. vagans* is known only from the type locality, Cape May Point, New Jersey, but if hunted for, it also should be found in other localities in New Jersey.

Gastrocopta sterkiana Pilsbry 1917

Gastrocopta procera sterkiana Pilsbry. Pilsbry, 1948: 908.

Gastrocopta procera (Gould) has the lower palatal fold deeply immersed, high, narrow, and nearly horizontal; while in *G. sterkiana* the lower palatal fold is lower down, broader, lower, and sets at an angle of about 45°. The range of *G. sterkiana* is mostly west of the range of *G. procera*, from Oklahoma and Texas westward.

Gastrocopta riparia Hubricht 1978

Gastrocopta procera form *riparia* Pilsbry. Pilsbry, 1916: 65, pl. 12, fig. 6; 1948: 908.

Gastrocopta riparia has the lower palatal fold as in *G. sterkiana*, but the columellar lamella is shorter and without the nodule below it. The shell is shorter than in *G. procera* and has a more distinct taper. It is a species of the Gulf Coastal Plain, ranging from southern Texas to Florida.

Gastrocopta servilis (Gould 1843)

Pupa servilis Gould. Gould, 1843: 356.
Gastrocopta servilis (Gould). Pilsbry, 1916: 70.

I have collected *G. servilis* at several places in Florida and have found old lots in museums, so that it is not a recent arrival. It resembles *G. rupicola* (Say), but is larger and darker colored. It usually lives in open grassy places, roadsides, lawns and dumps. I have collected it in Hamilton, Highlands, Manatee, Sarasota, Lee, Collier, Dade and Monroe Counties, Florida.

Carychium riparium new species
Fig. 41

Description. Shell minute, elongata, rimate, whitish, thin, glossy; spire conical, first whorl bluntly rounded; whorls 5 to 5.5, nearly smooth, or weakly striate, convex, sutures distinct; aperture about two-fifths the length of the shell, ovate; basal lip reflected, outer lip expanded, sinuous, thickened within; on the parietal margin near its junction with the columella there is a distinct lamella which extends inward in an even spiral around the columella, below this is another lamella which starts abruptly about one-half whorl in, and extends into the penultimate whorl.

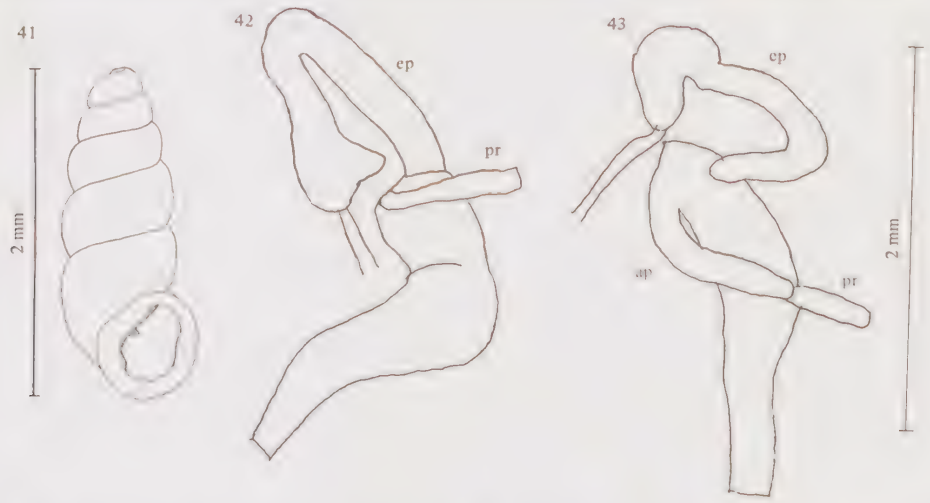


FIG. 41, *Carychium riparium* Hubricht, Holotype. FIG. 42, *Paravitrea tiara* Hubricht, penis and accessories. FIG. 43, *Paravitrea alethia* Hubricht, penis and accessories.

Height 2.0 mm, diameter 0.8 mm, aperture height 0.8 mm, aperture width 0.6 mm, 5.5 whorls. Holotype.

Distribution. *Kentucky:* Meade Co.: near Doe Run, 3 miles east of Brandenburg (Type Locality), Holotype 171659, Paratypes 171658, FMNH, other Paratypes 19566, collection of the author. Jefferson Co.: near Middle Fork Beargrass Creek, at Grinstead Drive, Louisville. Edmonson Co.: Mammoth Cave National Park: Green River floodplain, near River Styx; near Robbins Branch; ravine, 1.5 miles north of Brownsville. *Indiana:* Clark Co.: near Fourteen Mile Creek, 3 miles northeast of Charlestown.

Remarks. *Carychium riparium* is most likely to be confused with *C. exile* H. C. Lea. It differs in its more opaque shell, more conical spire, weaker sculpture and expanded rather than reflected outer lip. It averages smaller and more slender. The smaller specimens are almost as small as *C. nannodes* Clapp. In its sculpture and whitish shell it resembles *C. exiguum* (Say). In its internal lamellae it resembles *C. nannodes.* At the type locality and in Clark Co., Indiana, it was found associated with both *C. exile* and *C. exiguum.*

Opisthosiphon bahamensis (Pfeiffer 1865)

Opisthosiphon bahamensis (Pfeiffer). Pilsbry, 1948: 1077.

This species was collected at Key West, Florida, about 80 years ago, but it has not been found since. It was probably an introduction which did not survive. It should be removed from the list of native land snails.

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Malacological Review, 1977, 10: 53-58

INTRAMARSUPIAL SUPPRESSION OF FETAL DEVELOPMENT IN SPHAERIID CLAMS

Claus Meier-Brook

ABSTRACT

Sphaeriid clams of the genus *Pisidium*, which have brood care in their interlamellar chambers, deposit more eggs in the inner gills than develop until birth size. From the fetal larval stage on, generally 1/2 of the embryos continue growth until birth at a length of about 0.9 mm, whereas the remaining ones stay about 0.2 mm long. These last individuals do not continue development later, but disappear as a non-viable stage around the birth period. The agent responsible for suppression of development is likely to be of chemical nature.

Inhibition of development in embryos within the maternal uteri or organs of similar function has been reported in various groups of animals (Burton, 1957; Steel, 1961), but not hitherto in mollusks. Among the various taxa of this phylum, which have developed brood care, the freshwater clam family Sphaeriidae is the first one where such a phenomenon can be demonstrated.

The 3 nearly cosmopolitan genera of the family Sphaeriidae are *Sphaerium* Scopoli 1777, *Musculium* Link 1807, both commonly known as fingernail clams, and *Pisidium* C. Pfeiffer 1821, or pill clams. The former 2 genera generally attain a length of 12 to 20 mm, while most of the *Pisidium* species do not exceed a length of 5 or, in some cases, only 2 mm. All members are hermaphrodites. After fertilization in the spermoviduct (Odhner, 1929; Meier-Brook, 1970: 94) eggs pass into chambers formed by the inner demibranchs of each side and the walls of the visceral sac. Here they find preformed sites where they penetrate between the gill filaments with ease (Meier-Brook, 1970: 97). The gill tissue begins to grow over them, thus forming a brood sac. In *Sphaerium* and *Musculium* the young are born at a length of 2 to 5 mm; in *Pisidium* they are usually born at a length of 0.9 to 1.1 mm. The brood sac tissue at first increases in size with the growth of the embryos[1]; but later it is strained and finally ruptured by the growing young. In *Pisidium*, for example, this occurs when the embryos are about 0.7 mm long. They spend the last 0.2 to 0.4 mm of growth before birth, lying free in the interlamellar chamber (Meier-Brook, 1970). At this stage the parental animals are sometimes not much longer than twice the length of their young, of which more than 1 is usually present.

Previous investigators have stated that often a gravid *Sphaerium* contains so many developing young that these would in no case have sufficient space to develop until birth (Groenewegen, 1926). As a solution to the problem, Groenewegen hypothesized that the youngest embryos are retarded in growth until the oldest ones leave the interlamellar chambers, thus providing room for the further development of the younger, smaller ones. Indeed in gravid fingernail clams embryos of several different stages can be observed at any time, which would be in line with this supposition. But since development of one brood is not completed before the next set of eggs is deposited in the inner gills and mature animals of *Sphaerium* and *Musculium* are continuously gravid, a clear decision of whether or not embryos of different sizes within the same parent belong to the same brood cannot be made. Newly deposited eggs are not able to enter existing brood sacs, and must form new ones.

[1] To facilitate the description all developmental stages from the zygote to birth size are herein called "embryos".

On the other hand, the tissues of brood sacs touching each other show a capacity to fuse together; therefore it could not be excluded that fusion of sacs accounts for size differences of young within a common sac. Groenewegen's hypothesis mentioned above could not be examined because small embryos found in brood sacs can either be remnants of a previous brood or members of a recent one.

A final possibility of explaining the occurrence of distinctly different developmental stages in the same brood sac would be to assume mutual growth inhibition between embryos leading to some reaching birth and others perishing. Recently Heard (1976) expressed a suggestion like this in the case of *Sphaerium* and *Musculium*. He said: "It is possible that some 'retarded' F_1 never complete their development, dying before birth." He continued: "However, the occasional occurrence of different size groups of extramarsupial larvae (mature larvae that have escaped from the brood sacs) in the same demibranch suggest that some of these retarded F_1 will complete development and are born at a smaller size than their siblings that matured in the same sac." Only a quite recent observation by Mackie et al. (1976) clearly demonstrated that in the North American *Musculium securis* (Prime) "not all larvae are viable. Some fetal and prodissoconch larvae die before reaching the extramarsupial stage."

Since these open questions do not adequately explain the phenomenon of different-sized young in the same brood sac, it was necessary to find instances which met the following requirements: 1) Exclusion of migration of less developed, younger embryos from one brood sac to another one, after fusion of brood sacs; 2) Examination of species or populations which do not breed continuously and which, whenever possible, have a reproductive season that is restricted to the development of one brood at a time, synchronized as strictly as possible within a population.

Members of the genus *Pisidium* meet the 1st condition since, in all known cases, they have only 1 brood sac in each demibranch. The 2nd condition is not as readily encountered; pisidia include a broad variety of life histories, from semelparity to continuous iteroparity, depending on internal or external factors (Meier-Brook, 1970). The most suitable localities at which to look for such populations would be waters where the warm season is long enough to permit maintenance of the population, but short enough to provide for high synchronization of individuals, i.e., for a clam population to start and to end a single incubation period as simultaneously as possible. These climatic conditions are found in Europe either in the far North or in higher altitudes of the mountains. Sublittoral zones of some lakes in the Black Forest, around 1000 m above sea-level, harbour populations of *Pisidium* with those characters.

Pisidium lilljeborgii 'Clessin' Esmark & Hoyer, collected in a depth of 4-6 m, deposit eggs from mid-April to the end of May. After an incubation period of 2 1/2 to 3 1/2 months, the last developing young in the population are born, mostly before August. During the first 1 1/2 months all embryos are of a more or less spherical shape, with a diameter of <0.3 mm. All embryos in the same parental individual then have a nearly identical size. One month later, a distinct divergence in growth of embryos can be observed. Part of a brood has reached the prodissoconch stage with shells 0.3 to 0.7 mm long; another part of the brood in the same sac has stopped growth at a size of 0.15 to 0.2 (exceptionally to 0.25) mm. In Heard's classification, this is the stage of fetal larva, which, however, comprises a wide range of developmental stages. As the larger young continue to grow, the retarded embryos are often pressed against the brood sac wall and slightly flattened.

After the larger embryos have ruptured the brood sac and increasingly diminished the sac tissue which they use for nutrition (Meier-Brook, 1970: 100), the retarded embryos usually disappear. Only in exceptional cases can such an embryo be observed in a corner of the remains of the sac. In August, when the last young clams are born, or in later months, I have never found a younger embryo that could be interpreted as a previously retarded young.

In determining the maximum number of embryos per parental individual soon after the release of the eggs in the demibranchs, one may find up to 13 in the investigated population of *Pisidium lilljeborgii*. The maximum number of embryos distinctly longer than 0.2 mm and thus having a chance of completing development was in no case >8. Still more distinct are the differences in *P. hibernicum* Westerlund, in a sample from the same lake. In many gravid animals the maximum number of embryos beginning development is 5; one specimen had 6 and one had 8 embryos. No more than 2 of these, however, were ever found to complete their development until birth. The example of *P. obtusale* (Lamarck) from a neighbouring bog in the Black Forest (Fig. 1) demonstrates that the final numbers of embryos from the low to the high size classes of parental animals (P) follow approximately the same slope as the initial numbers do. In this example, adults of any length deposit 3 eggs more than they properly could support.

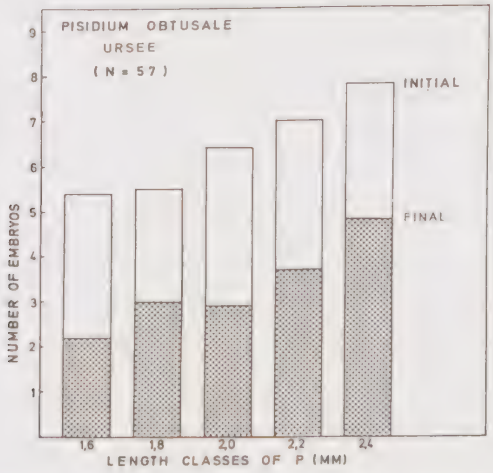

FIG. 1. Brood sizes in different size (length in mm) classes of gravid *Pisidium obtusale* (Lamarck) in Ursee, southwestern Germany; 6 April and 16 June 1964: Initial (whole columns) and final (dotted portions) embryo numbers.

To give figures for entire populations, I have calculated mean values for initial and final numbers of embryos from samples yielding sufficient data (Table 1). In littoral species of *Pisidium* about half the brood reaches birth, whereas in the profundal species, *P. conventus* Clessin, nearly 2/3 of the embryos complete development until birth.

There is little doubt that further development of the smaller embryos is suppressed by the more advanced ones, and that without this suppression embryos within the brood sacs would be competing with each other, at least for space, if not for nourishment as well. How may the phenomenon reported here have developed during evolution? Does it have a selective advantage? One could suppose that a pre-selection takes place here which favours the stronger and faster growing young. But such a selection would be much more efficient after birth, when the environment can act upon individuals immediately. The phenomenon can rather be understood as a consequence of size reduction during the evolution: Taxonomists agree that *Pisidium* are descendants from the larger-sized *Sphaerium*. With the considerable size reduction accompanying the evolution of pisidia, a joint reduction of demibranchs and a certain, but obviously insufficient, reduction of birth size took place. On the other hand, gonad productivity remained at a relatively high level, so that competition between developing young resulted as a possible consequence of modified conditions. Since there was evidently no alternative, following the course of intramarsupial suppression did

TABLE 1. Initial and final brood sizes in 4 *Pisidium* populations in lakes of High Black Forest, southwestern Germany, and *P. amnicum* from northern Germany (Castrop-Rauxel, W. Hinz leg; cp. Danneel & Hinz, 1976). n, numbers of gravid animals examined; s.d., standard deviation.

Population	Sampling dates	n	Embryo number				Dying before birth
			Initial		Final		
			range	mean ± s.d.	range	mean ± s.d.	
P. obtusale, Ursee	6-IV + 16-VI 1964	57	4-10	6.3 ± 1.6	2-8	3.2 ± 1.4	49%
P. lilljeborgii, Titisee	12-VIII-64	47	3-13	6.2 ± 2.3	1-8	3.2 ± 1.4	49%
P. hibernicum, Titisee	12-VIII-64	28	1-8	3.1 ± 1.7	1-2	1.7 ± 0.4	46%
P. conventus, Titisee 13 m	throughout 1964	21	2-6	4.3 ± 1.1	1-5	2.7 ± 1.1	38%
P. amnicum, Rhein-Herne-Canal	23-XII-72	13	5-41	15.9 ± 9.6	3-37	11.9 ± 8.9	27%[1]

[1] Extremely variable: 0-54%!

not mean a selective disadvantage.

After the occurrence of this phenomenon became evident I examined the European species, including *Pisidium amnicum* (Müller), one of the largest species with the closest anatomical relationship to *Sphaerium*. All Holoarctic species examined show divergence of embryo growth which must be interpreted in the same way. There is evidence that this is a common process in the entire genus. At present I have been able to examine only 1 species, where the phenomenon described was not found, viz., in *P. forense* Meier-Brook from Brazil.

What may be the reason that such a process has not been noted before? Most workers examined *Sphaerium* and *Musculium* as representatives of sphaeriid life histories. I have pointed out the difficulties in interpreting findings in these genera. The first author to deal with brood size in *Pisidium* systematically was Heard (1964; 1965), who repeatedly emphasized that "all embryos in the same parent are nearly equal in size". Indeed, this holds true for prodissoconch and extramarsupial embryos. His methods of investigation, however, did not permit him to find any smaller embryos besides these, as retarded embryos do not yet possess a shell. While in the present study all animals of a life history sample were dissected individually, Heard determined brood size by the so-called isolation-rotting-technique: he isolated the adults in glass bottles with water, and after the tissues had decayed he counted and measured the remaining shells of embryos. In only few cases did he dissect a few preserved specimens, in which he might by chance have found only 1st or 2nd stage embryos. But in these stages a distinctly divergent growth would not yet have taken place. Thus it is impossible to judge whether the many figures of brood size reported in previous papers mean the numbers of embryos beginning development or those having a chance to survive until birth.

The only author who reported the existence of different size classes of embryos of pisidia in the same parent was Thut (1969). He observed this in *Pisidium casertanum* (Poli), but did not further comment on it. It is unlikely, however, that these size classes represented members of different broods that overlapped in development as in *Sphaerium* and *Musculium*.

One may ask what sort of mechanism may be involved in the phenomenon reported here. I have observed that sometimes retarded embryos are pressed and flattened by larger, shell-bearing ones. But on the other hand, I have regularly found retarded embryos lying in remote corners of a brood sac; they did not show any sign of a mechanical pressure. My

conclusion is that a chemical component dissolved in the fluid filling the brood sacs plays a role as a growth inhibitor similar to those substances which effect regulation of population density in natural communities. I may call the pioneer experiments of Rose & Rose (1965) to the reader's mind. These authors concluded that tadpoles produce an excretion in amounts proportional to their body weights. Younger tadpoles are more sensitive than older ones to a certain concentration of that substance. Thus when population density is increasing too much, any divergence in growth must result in growth inhibition in the smaller larvae at first, favoring the advanced individuals.

In addition, metabolic products with similar effects have been found in several groups of freshwater organisms, among others in snails of the genus *Biomphalaria* serving as intermediate hosts of schistosomes (Berrie & Visser, 1963). I expect that growth inhibition of embryos in *Pisidium* is due to a similar physiological process. At least it cannot be compared with the phenomenon known from the egg capsules of some prosobranch snails where only one or a few eggs develop at the cost of all the others which serve them as nutrient eggs. In my opinion it is rather more comparable to observations in hares where up to 16% or even 60% of the young embryos have been found to be reabsorbed by the maternal tissues (Burton, 1957).

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ANATOMICAL SYSTEMATICS OF *CRISTARIA PLICATA* (LEACH) (PELECYPODA: UNIONIDAE: UNIONINAE)[1,2]

William H. Heard

ABSTRACT

The anatomy of *Dispas plicatus* Leach, the type species of the Asian naiad genus *Cristaria* Schumacher, is described from 3 growth forms from a common population. The findings are employed in characterizing *Cristaria* as members of the Unionidae: Unioninae s.s., and in interpreting the phylogenetic position of that nominate subfamily within the Unionidae.

Significant character states include unipartite septa and water-tubes in the outer, marsupial demibranchs, dimorphic septal spacing between outer and inner demibranchs of females but not males and notably within the marsupial demibranchs, vestigial septal perforations, subtriangular, hooked glochidia and concentric beak sculpture. Specializations are reduction in the sizes of the supra-excurrent opening and the foot, and vestigial hinge dentition.

The Asian Lamellidentinae are proposed as being ancestral to the Unioninae s.s., among which *Cristaria*, in comparison to *Unio*, are considered to be derived. It is also suggested that the Anodontinae s.l. were derived from the Unioninae s.s.

INTRODUCTION

The generic-group taxon *Cristaria* Schumacher 1817 (type species, by monotypy: *C. tuberculata* Schumacher 1817) replaced by objective synonymy the name *Dispas* Leach 1815 (type, by monotypy: *D. plicatus* Leach 1815), which Laurenti (1768) had previously applied to a group of reptiles. Haas (1969a) characterized Recent members of this eastern and southeastern Asian group of freshwater mussels as comprising 2 subgenera (*Cristaria* s.s. and *Pletholophus*), 3 species and 2 subspecies. Modell (1964) cited *Cristaria* from Oligocene to mid-Miocene deposits in Japan, the Miocene to Upper Pliocene of northern Baikal and the Upper Pleistocene of northern China, and *Pletholophus* (treated as a genus of Unionidae:Anondontinae) from Oligocene beds in Japan. Haas (1969b) simply noted Tertiary to Recent *Cristaria* s.s. from eastern Asia, and only Recent *C. (Pletholophus)* in eastern and southeastern Asia.

Simpson (1900, 1914) placed *Cristaria* in the Unionidae:Unioninae:Heterogenae (the latter name represents a division of the Unionidae:Lampsilinae; see Heard & Guckert, 1970; Burch, 1975). The genus was subsequently classified in the Unionidae:Anodontinae by Thiele (1934), Haas (1969a,b) and Starobogatov (1970), and in the Unionidae:Hyriopsinae by Modell (1942, 1964), and in the Amblemidae:Hyriopsinae by Brandt (1974).

All of the above records and classifications were based on shell features, but, as noted by Heard & Guckert (1970), classifications of naiades based on hard-part morphology may differ significantly from those founded on soft-part anatomy and on reproductive features.

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[1]This investigation was supported, in part, by the Smithsonian Institution's "Waterborne Diseases of the Mekong River Drainage" research project.

[2]This paper is dedicated to Dr. J.P.E. Morrison in honor of his many contributions to malacology prior to his retirement on 31 July 1975.

The purposes of this report are to describe what I consider to be the systematically significant animal features of the type species of *Cristaria* and to provide an interpretation of the systematic position and affinities of this genus and of the subfamily of which it is a member.

MATERIAL AND METHODS

This report is based on a single collection of 16 animals made on 10 July 1971 from Kut Kwang, a lake about 0.5 km southwest of Ban Kut Kwang (7.2 km south of Khon Kaen on Highway 2), Khon Kaen Province, Thailand. The shells of these animals have been deposited in the U.S. National Museum of Natural History, and empty shells from the same collection are in the Thai National Reference Collection, Bangkok.

The methods employed here are those described by Heard (1975) and Heard & Vail (1976). Most anatomical features were revealed by gross dissection, although details of the structural organization of the demibranchs and also the sex of each individual were determined by histological sections.

SHELLS

Three shell forms occurred in the material examined: 4 males and 4 females of a smaller, more alate type (Fig. 1), 3 males and 3 females of a larger, more ovate type (Fig. 2), and 1 male and 1 female of intermediate size and shape (see Table 1). The anatomies of these forms differed only in some size relationships, and, because the anterior and especially the posterior wing of the shell could have been broken off or worn down with increased age (such a condition is particularly notable in the unionid *Hyriopsis bialata* Simpson; pers. observ.), I believe that these variations reflect allometric changes. The anatomical descrip-

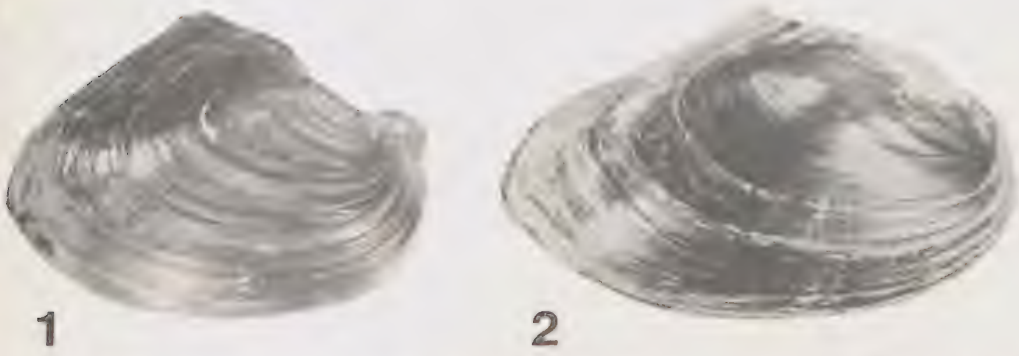
TABLE 1. Size relationships (mean ±1 standard deviation) in mm of 3 "forms" of *Cristaria plicata*.

Length	Form		
	Small, alate (N = 8[1])	"Intermediate" (N = 2)	Large, ovate (N = 6)
Shell length[2]	103.77 ± 10.57	130.50 ± 9.19	150.66 ± 8.53
Length of SO[3]	13.14 ± 2.35	11.30 ± 5.51	9.97 ± 2.24
Length of PS	25.81 ± 2.90	30.60 ± 4.38	31.38 ± 2.98
Length of EO	8.10 ± 1.47	8.95 ± 1.06	11.03 ± 0.90
Length of IO	14.87 ± 1.42	20.80 ± 0.99	26.12 ± 1.20

[1] In 1 female the supra-excurrent opening was obliterated by the pallial suture (total length: 46.3 mm).

[2] Up to 300 mm *fide* Haas (1969a). Thai specimens rarely exceed 160 mm in length (Brandt, 1974).

[3] EO = excurrent opening; IO = incurrent opening; N = number of specimens; PS = pallial suture; SO = supra-excurrent opening.



FIGS. 1-2. Right valve of *Cristaria plicata.* FIG. 1. Small, alate form; 100.0 mm long. FIG. 2. Large, ovate form; 161.0 mm long. (Animals from these shells are depicted in Figs. 3-4.)

tion given here is common to the animals of all 3 shell forms unless stated otherwise.

Beak sculpture, reported by Simpson (1900,1914), Modell (1942), Haas (1969a,b) and Brandt (1974) to be initially double-looped and subsequently concentric single-looped ridges, was obliterated by decoriation in all but 1 specimen. The beak sculpture on this specimen consisted of fine, single-looped, low concentric ridges toward the ventral part of the beaks, and was followed onto the upper part of the disc by several low but wide, distantly spaced, concentric bars. However, although concentric, these ridges and bars were not parallel to the growth striae but lay at a slight angle to them (see Fig. 1).

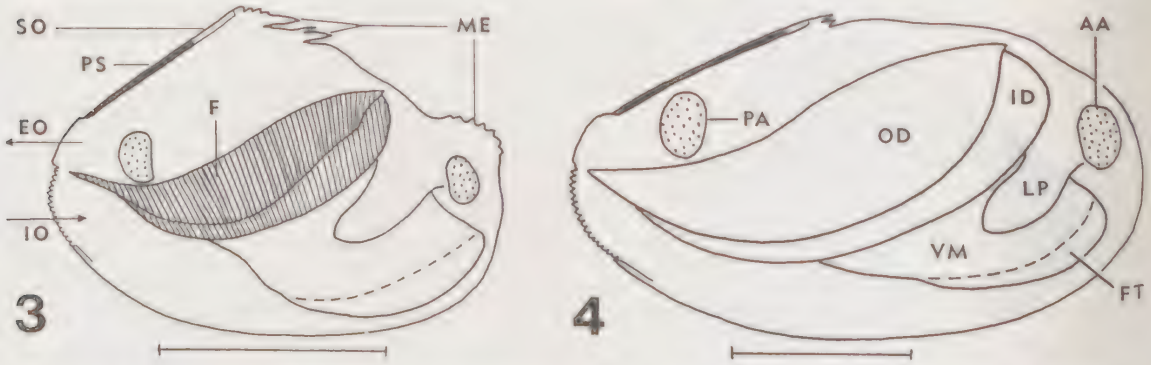
Prior workers presented varying descriptions of hinge dentition. Simpson (1900, 1914) recorded the presence or absence of a faint pseudocardinal tooth in each valve and the presence (or absence in "adult shells") of a single, short lateral tooth in each valve. Modell (1942, 1964) did not treat features of this genus or species, but noted a loss of the pseudocardinals within the Hyriopsinae, in which he placed *Cristaria* with *Hyriopsis.* Whereas Brandt (1974) cited obsolete pseudocardinals and strong, long, lamelliform laterals, Haas (1969a,b) previously considered all such prominences to be claustra, viz., structures presumably only analogous to hinge teeth. It is evident that there is considerable intraspecific variation in *C. plicata,* because all 16 shells examined here were entirely edentulous.

ANATOMY

Mantle

The small anterior wing and the more prominent posterior wing of the small, alate shell form contained thin extensions of the mantle (Fig. 3: ME) that were dorsally crenulated and horizontally cleft, respectively. In the large, ovate form (Fig. 4) the wings of the shell were missing, the anterior mantle extension was absent, and the incised posterior mantle extension was reduced in size. The mantle extensions in the specimens of intermediate size and shape were only moderately developed.

A pallial suture (Figs. 3, 5: PS), about 3 times longer than the excurrent opening (EO), separated the latter from the supra-excurrent (supra-anal) opening (SO). The excurrent opening was about slightly more (alate form) to slightly less (ovate form) than 1/2 as long as the incurrent opening (IO), and was nearly 2/3 of (alate form) to slightly greater than (ovate form) the length of the supra-excurrent opening. The incurrent opening was only slightly (alate form) to about 2½ times longer (ovate form) than the supra-excurrent opening. These variations reflect changes in proportion with size (age): decrease in the supra-



FIGS. 3-4. Dextro-lateral aspect of the animal of *Cristaria plicata*, with the mantle removed from over the branchial chamber. FIG. 3. Small, alate form. FIG. 4. Large, ovate form. Scale: 50 mm for each figure. (Shells of these animals are shown in Figs. 1-2.) AA = anterior adductor muscle; EO = excurrent (anal) opening; F = filament; FT = foot; ID = inner demibranch; IO = incurrent (branchial) opening; LP = labial palp; ME = mantle extension into wing; OD = outer demibranch; PA = posterior adductor muscle; PS = pallial suture; SO = supra-excurrent (supra-anal) opening.

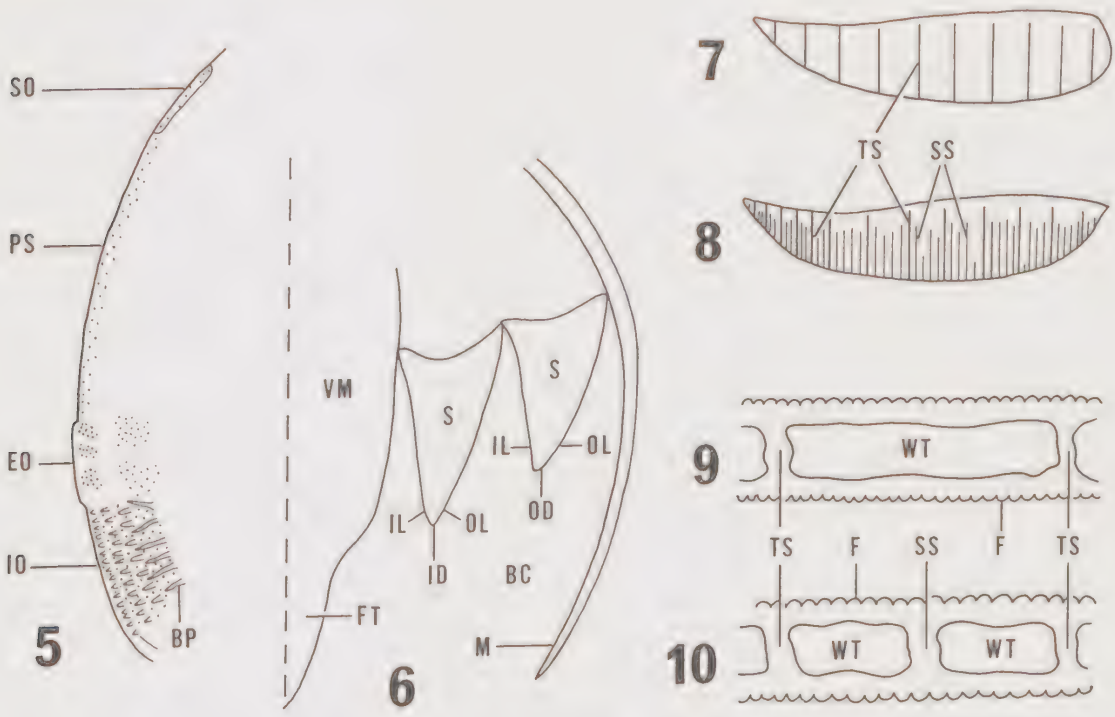
excurrent opening and concomitant increase in the pallial suture, slight elongation of the excurrent opening, and significant lengthening of the incurrent opening (see Table 1). The ventral margins of the mantle sheets were free (i.e., not conjoined) anterior to the incurrent opening.

The inner surface of the inner lobe of the mantle margin was simple (i.e., lacked papillae), except at the incurrent opening. The incurrent, branchial papillae (Fig. 5: BP) were usually tereted and only rarely bifid apically, and were arranged in 4 rows. The anterior-most row had the largest and fewest papillae, and the sizes decreased and numbers increased toward the posterior-most row.

The pigmentation pattern on the inner surface of the inner lobe of the mantle sheets was nearly constant in preserved animals (see Fig. 5). A faint dusting of brown pigment formed a very narrow band along the apex of the supra-excurrent opening (SO) and the adjacent pallial suture (PS). The low flaps of the excurrent opening (EO) had a white apex, small blotches of moderately concentrated black, melanistic pigment immediately anterior to the apex, and, anterior-most, large blotches of light dustings of melanin. The incurrent opening (IO) had a white background color that was covered by a faint to light dusting of melanin between the papillae, and by rust-orange pigment on the papillae (heavy concentration on the anterior-most row, to faint on the posterior-most row).

Demibranchs

The dorsal margin of the outer lamella (Fig. 6: OL) of the outer demibranchs (OD) was united for its entire length with the inner surface of the mantle, thereby creating a complete diaphragm that separated the branchial chamber from the suprabranchial chamber. The dorsal margin of the inner lamella (IL) of the outer demibranchs (OD) was joined for its entire length to the dorsal margin of the apposing outer lamella (OL) of the inner demibranchs (ID). The dorsal margin of the inner lamella (IL) of each inner demibranch (ID) was attached to the visceral mass (VM) for about its anterior-most 1/8 to 1/6 of its length in the alate form and 1/10 to 1/7 in the ovate form, was free from the visceral mass for the next posterior 1/3 to nearly 1/2 of its length in the alate form and about 1/2 in the ovate form, and was united, behind the visceral mass, with the dorsal margin of the other inner demibranch for nearly the posterior-most 1/2 of its length in the alate form and for nearly



FIGS. 5-10. Posterior mantle openings and gills in *Cristaria*. FIG. 5. Posterior mantle openings in a large, ovate *Cristaria plicata*, with pigmentation pattern (described in the text) and papillae shown. BP = branchial papillae; EO = excurrent opening; IO = incurrent opening; PS = pallial suture; SO = supra-excurrent opening. FIG. 6. Transverse aspect of 1 side of *Cristaria plicata*. BC = branchial chamber; FT = foot; ID = inner demibranch; IL = inner lamella; M = mantle; OD = outer demibranch; OL = outer lamella; S = interlamellar septum; VM = visceral mass. FIGS. 7-8. Dextro-lateral representations of the right demibranchs of *Cristaria plicata*, with the outer lamella removed to show heights and spacing of interlamellar septa. Fig. 7. Non-marsupial demibranch (all 4 in males, but only inner pair in females). Fig. 8. Marsupial, outer demibranch with organization of most females. SS = short septa (densely spaced); TS = tall septa (typically distantly spaced, but more crowded in posterior end of female outer demibranchs). FIGS. 9-10. Frontal aspect of parts of different demibranchs of *Cristaria plicata*. Fig. 9. Non-marsupial demibranch. Fig. 10. Marsupial region of female outer demibranch. F = filament (in transverse section); SS = short septum; TS = tall septum; WT = water-tube.

1/3 to almost 1/2 in the ovate form.

The outer lamellae of both inner and outer demibranchs were higher than the inner lamellae (see Fig. 6), and each lamella of the inner demibranch was higher than the corresponding lamella of the outer demibranch. The interlamellar septa (S) in the inner demibranchs were higher than those in the outer demibranchs in 12 of the 16 animals, and slightly lower in the others.

The interlamellar connections in all 4 demibranchs of both males and females were developed as septa (Figs. 6-10: S, SS, TS) that ran parallel to the filaments (Fig. 3: F). The septa showed 3 kinds of variation: tall (about 4/5 to 9/10 as high as the inner lamella) or short (about 1/10 to 7/10 as high as the tall septa), comparatively distant or dense spacing, and imperforate or perforated constitution. The tall septa (TS) were distantly spaced in all demibranchs of both sexes (Figs. 7-10), but were more crowded in the posterior 1/5 of the female outer demibranchs. Several short septa (SS) occurred between consecutive

tall septa throughout the outer demibranchs of most females (Fig. 8) but only for the middle 3/5 and 1/10 of the length of these demibranchs in 1 alate and 1 "intermediate" female, respectively; in all of these cases the short septa were densely spaced. Short septa in all non-marsupial demibranchs were rare and of sporadic distribution. The water-tubes (Figs. 9-10: WT) were flanked laterally by about 20 filaments (F) between distantly spaced septa, by about 10 filaments between the tall septa in the posterior 1/5 of female outer demibranchs, and by only about 6 filaments between densely spaced septa (Table 2). Most septa in all demibranchs of both sexes were continuous and complete (i.e., imperforate), although the densely spaced septa in the female outer demibranchs had a faint trace of a vertical row of up to 11 apparently closed performations. Rarely, a single, small, open performation was found in a densely spaced septum in the middle or anterior of 3 female outer demibranchs, and also in a middle, distantly spaced septum of some outer (1 specimen) and inner demibranchs (3 specimens) of some males.

All septa and water-tubes of all demibranchs of both males and females were simple, i.e., not vertically divided as in the marsupial demibranchs of the Unionidae:Anodontinae (see Heard & Guckert, 1970; Heard, 1975). None of the 8 females was gravid, but comparison of the structural organization of the 4 female demibranchs suggests that the marsupia are located in just the outer demibranchs, and perhaps only in the region of the densely

TABLE 2. Numbers of filaments flanking water-tubes in different demibranchs of *Cristaria plicata* (mean ± 1 standard deviation; based on 10 water-tubes for each condition).

Shell form / Part of demibranch	Outer Demibranchs		Inner Demibranchs	
	Males	Females	Males	Females
Small, alate				
Central, dorsal	24.90 ± 4.04	6.40 ± 1.58	24.20 ± 5.83	23.70 ± 2.21
Central, ventral		6.60 ± 2.12		
Posterior, dorsal		11.00 ± 2.40		
Posterior, ventral		6.10 ± 1.37		
"Intermediate"				
Central, dorsal	21.70 ± 3.59	6.50 ± 1.08	23.20 ± 4.49	21.00 ± 3.13
Central, ventral		6.50 ± 1.58		
Posterior, dorsal		10.50 ± 2.32		
Posterior, ventral		5.20 ± 0.79		
Large, ovate				
Central, dorsal	20.00 ± 3.94	6.20 ± 1.47	21.40 ± 3.20	24.50 ± 3.75
Central, ventral		6.70 ± 1.77		
Posterior, dorsal		10.20 ± 2.39		
Posterior, ventral		6.10 ± 1.37		

spaced septa as is the case in many other mussels in southeastern Asia (Heard, unpubl.).

Labial palpi

The palpi (Fig. 4: LP) were slightly more than 1/3 to nearly 1/2 as long as the inner demibranchs, and were not contiguous with them. The outer member of each palp was laterally attached to the inner surface of the mantle for about 1/3 to nearly 2/3 of its length in the alate form, and for slightly more than 1/2 of its length in the ovate form. The 2 members of each palp were dorsally joined together for almost their entire length in all forms.

Foot

These naiades were collected from near the center of a large, shallow lake (< 2 m maximum depth). The substrate in which the animals were nearly completely buried was a very soft muddy silt. A very conspicuous anatomical feature of all of the animals was a very small foot, which suggests that they are poor burrowers except in such soft substrates. I did not find this species in harder, sand substrates at more than 150 other localities (mostly streams, and some other lakes) in northeastern Thailand.

LARVAE

Haas (1922) described and illustrated subtriangular, hooked glochidia from Chinese *Cristaria plicata*, as did Inaba (1941) and Higashi & Hayashi (1964) from Japanese material. Only Haas mentioned the presence of a larval thread, and only Inaba noted the existence of minute spines on the hooks. The larval valves in each study were higher (up to 338 μm) than long (up to 309 μm). In addition, Higashi & Hayashi recorded the presence of glochidia in November through March and their absence in the rest of the year, and estimated up to 500,000 glochidia per animal of 100-135 mm in length.

Eight of the present 16 animals were females, and the rest were males; no hermaphrodites were present. Morphologically mature gametes were present in each animal, but none of the females was gravid.

OTHER FEATURES

No digenetic trematode larvae or aspidogastrean trematodes were found in any of the 16 mussels, but nymphal and adult stages of an unidentified unionicolid water-mite were observed between the demibranchs of 14 of the animals.

DISCUSSION

Intraspecific variation

Basing his description on specimens from China, Haas (1922) provided a prior anatomical account of *Cristaria plicata*. The present findings agree with those of Haas except in terms of the relative size of the posterior mantle openings and pallial suture, his report that the inner lamella of the inner demibranchs was attached to the visceral mass, and his statement that the marsupia occupied the entire outer demibranchs. Moreover, although he described general variation in septal height and spacing (without mention of presence or absence of perforations), Haas' illustration of a marsupial demibranch shows the absence of short septa in both ends.

The discrepancy between these accounts of the attachment of the inner demibranchs

to the visceral mass or their detachment from it is enigmatic. Interspecific, congeneric variation in this feature is otherwise known only in the Nearctic genus *Strophitus* (Unionidae: Anodontinae; Heard & Fuller, unpubl.), but intraspecific variation has not been hitherto reported.

Interspecific variation

Knowledge of interspecific anatomical variation in *Cristaria* is provided by Haas' (1922) description of Taiwanese *C. discoidea* (Lea), the type species of the subgenus *Pletholophus*, and by Inaba's (1941) description of glochidia from Korean material of the same species. Wings and mantle extensions are lacking in *C. discoidea*. Although there is dimorphic septal spacing between the inner (distant) and outer (dense) demibranchs of females, short septa are evidently entirely absent. The glochidia are smaller (up to 277 μm high and 259 μm long) than in *C. (C.) plicata*. As also for the latter, Haas reported the attachment of the inner demibranchs to the visceral mass, failed to note the presence or absence of septal perforations, and concluded from non-gravid animals that the entire outer demibranchs serve as marsupia. Haas stated that his *C. discoidea* had been poorly preserved, but, if his findings are accurate, this is the first known case among naiades of congeneric variation in the presence or absence of short septa in marsupial demibranchs.

Generic comparisons

Other Asian mussels with subtriangular, hooked glochidia are members of *Anodonta, Inversidens, Lanceolaria, Simpsonella* and *Unio;* all but *Inversidens* are known to possess dimorphic septal spacing (Haas, 1922; Inaba, 1941; Higashi & Hayashi, 1964). Of these, the edentulous *Anodonta* have tripartite marsupial septa and water-tubes and variations of concentric beak sculpture (Ortmann, 1910a, 1912; Burch, 1975; Heard, 1975), and *Unio* have unipartite marsupial structure, complete hinge dentition and variations of zigzag beak sculpture (Haas, 1922; Heard & Vail, 1976). *Lanceolaria* and *Simpsonella* also have zigzag sculpture and presumably unipartite marsupial structure (see Haas, 1922), but, whereas *Lanceoloaria* have complete dentition, *Simpsonella* have only vestigial hinge teeth. *Inversidens,* with complete dentition but of unknown pattern of beak sculpture, have not been anatomically described, and reports on the larvae in this nominal genus are inconsistent. Inaba (1941) described subtriangular, hooked glochidia from the type species, *I. brandtii* (Kobelt), whereas Higashi & Hayashi (1964) recorded subovate, hookless glochidia from purportedly the same species; these workers described both kinds of larvae from among several alleged congeners of *Inversidens.* Such congeneric variation is unknown elsewhere among the naiades, and it is likely that both misidentification and misclassification created this confusion.

Among other anatomically described generic groups of Asian unionids, the larvae of *Cuneopsis* and *Schistodesmus* are unknown, the glochidia of *Acuticosta* are subovate and hookless but possess 2 tuberculated, truncated projections, and the glochidia of *Chamberlainia, Hyriopsis, Lamellidens, Physunio, Pseudoparreysia, Trapezoideus* and *Uniandra* (=*Contradens*) are subovate and hookless. All of these mussels have unipartite marsupial organization and dimorphic septal spacing, and at least *Hyriopsis, Lamellidens, Physunio, Trapezoideus* and *Uniandra* have perforated marsupial septa (Ortmann, 1911, 1916, 1917; Prashad, 1918a,b, 1919a; Haas, 1922; Bloomer, 1931; Woodward, 1964, 1965; Heard, 1974).

Although *Cristaria* and *Unio* differ in beak sculpture and hinge dentition, *Cristaria* are most similar to *Unio* in terms of larval and animal features. Included among the latter are septal perforations, which, however, appear to be secondarily vanishing in *C. plicata*. On the

other hand, the perforations may be of seasonal occurrence, as has been suggested for them in *Unio* (see Heard & Vail, 1976).

Subfamilial comparisons

Heard & Guckert (1970) characterized subfamilies of Nearctic naiades according to differences in anatomy, period of larval incubation, and presence or absence of hooks on the larval shell. Intrasubfamilial variation in larval form is known among mussels only in the Unionidae:Lampsilinae (viz., celtiform and hookless but 4-spined glochidia in *Proptera*, and subovate, hookless and lacking spines in all other groups; Ortmann, 1912), and Modell's (1942, 1964) and Brandt's (1974) placement of *Cristaria* with *Hyriopsis* in the Hyriopsinae seems unwarranted because the glochidia of *Hyriopsis* are subovate and hookless.

Subtriangular, hooked glochidia of the kind found in *Cristaria* are characteristic of the Unionidae:Unioninae s.s. [as restricted by Morrison (1955) and Heard & Guckert (1970); *non* Simpson (1900, 1914), Ortmann, 1910a, 1912), Modell (1942, 1964), Haas (1969a,b), *nec* Burch (1975)] and Anodontinae s.l. [*sensu* Ortmann, Heard & Guckert and Burch (=Anodontinae s.s. + Alasmodontinae *sensu* Modell, Morrison and Haas)]. Unionine *Unio* and anodontine *Strophitus* have in common dimorphic septal spacing and at least seasonally perforated marsupial septa (Heard & Vail, 1976, and Heard & Fuller, unpubl., respectively), but only the Anodontinae s.l. possess a tripartite marsupial organization with imperforate septa in all but some *Strophitus*. Morrison's (1955) listing of the tripartite condition for all Unionidae is in error. Although reduced hinge dentition is common among anodontine groups (see Haas, 1969a,b; Burch, 1975), unipartite marsupial structure relates *Cristaria* to the Unioninae s.s. (*sensu* Heard & Guckert), in which group this genus is herein placed.

Familial groupings

The present findings on dimorphic septal spacing between outer and inner demibranchs of female but not male *Cristaria plicata* support Haas' (1922) report that *C. plicata* and *C. discoidea* are exobranchous. That the marsupia occur in only the outer demibranchs confirms *Cristaria* as members of the Unionidae (*sensu* Heard & Guckert, 1970).

Ensidens, Harmandia, Indonaia, Lamprotula, Parreysia, Pilsbryoconcha, Pseudodon, Ptychorhynchus, Rectidens, Scabies and *Solenaia* (=*Balwantia*) are Asian members of the tetragenous Amblemidae (*sensu* Heard & Guckert, 1970), with subovate, hookless glochidia except in *Indonaia*, whose larvae are of uniquely heightened shape and have hooks (Ortmann, 1910b; Ghosh, 1918; Prashad, 1918b, 1919a,b; Haas, 1922; Woodward, 1969; Heard, 1974; Brandt, 1974).

Unfortunately, the nominal Asian genera *Arcidopsis, Arconaia, Caudiculatus, Ctenodesma, Diaurora, Discomya, Elongaria, Lepidodesma, Nannonaia, Oxynaia, Pressidens, Prohyriopsis, Protunio, Pseudobaphia, Radiatula, Rhombuniopsis, Schepmania* and *Unionetta* are known only from adult shell characters (see Haas, 1969a,b), and neither their relations to *Cristaria* nor even their familial memberships can yet be determined. Patterns of beak sculpture in these groups are: concentric in *Pressidens* and *Rhombuniopsis*, zigzag in *Ctenodesma, Diaurora, Oxynaia, Radiatula* and *Unionetta*, and unknown in the rest. All have complete hinge dentition, except in *Pseudobaphia* (laterals reduced) and *Lepidodesma* (all teeth vestigial).

Phylogenetic affinities

Despite discordance between shell and animal classifications of mussels, caused by convergence in either or possibly both sets of characters, and insufficient information about

many mussels, it is possible to advance interpretations of the systematic position of (1) *Cristaria* within the Unioninae s.s. and (2) the nominate subfamily within the Unionidae.

I consider the following features in *Cristaria* to be derived character states in comparison to the alternative conditions in *Unio*, the only other currently known group of unionine naiades: concentric beak sculpture, a nearly edentulous hinge, incipient elongation of the marsupial region of the outer demibranchs, incipient secondary loss (?) of septal perforations, incipient loss of the supra-excurrent opening due to elongation of the pallial suture below it, and reduced size of the foot. Even after omission from consideration of the conspicuous specializations (viz., reductions of the dentition, supra-excurrent opening and foot), *Cristaria* can be treated as "more advanced" than *Unio*.

Evaluation of the features of Asian groups necessitates a reinterpretation of the affinities of unionids as proposed by Heard & Guckert (1970: 343). Those workers concluded that the Unioninae s.s. may have evolved as a side branch of the line leading directly from the Pleurobeminae to the Anodontinae s.l., but they overlooked the existence of the Lamellidentinae Modell, 1942 (=Hyriopsinae =Contradentinae, both Modell, 1942). Members of that Asian group, containing *Chamberlainia, Hyriopsis, Lamellidens, Physunio, Pseudoparreysia, Trapezoideus* and *Uniandra,* are anatomically similar to the Unioninae s.s. in that all have unipartite marsupial structure, dimorphic septal spacing in the outer demibranchs and perforated marsupial septa, but differ from them by generating subovate, hookless glochidia (Ortmann, 1911, 1916, 1917; Prashad, 1918a,b, 1919a; Haas, 1922; Bloomer, 1931; Woodward, 1964, 1965; Heard, 1974). In addition, at least *Hyriopsis* and *Physunio* have long-term larval incubation (Heard, unpubl.), a feature of *Cristaria* (see Higashi & Hayashi, 1964) but not *Unio* (Heard & Vail, 1976). Finally, all lamellidentines but *Hyriopsis,* with delicate concentric ridges, have zigzag beak sculpture, and all have complete hinge dentition (Haas, 1969a; Brandt, 1974).

Asian (or other?) Lamellidentinae probably gave rise independently to the Unioninae s.s. of the Eastern Hemisphere and to the Nearctic Pleurobeminae (=Popenaiadinae) and Lampsilinae. These evolutions, for which detailed documentation will be published separately, involved changes in septal structure and organization and also marsupial size in the outer demibranchs in the latter 2 groups, and in larval form in the derivation of the Unioninae s.s. The Anodontinae s.l. (represented throughout the Northern Hemisphere, but of significantly greater generic and species diversity in the Nearctic Region) were most likely derived from the Unioninae s.s. through the assumption of tripartite marsupial organization and, in the majority of species, by elongation of the marsupia and loss of septal perforations. Indeed, tripartite marsupia comprise the only significant structural feature (of animal or shell) that distinguishes the anodontine *Strophitus* from the unionine *Cristaria*. That *Hyriopsis* and *Physunio* have long-term larval incubation, whereas most unionines (viz., *Unio*) display short-term incubation, does not invalidate these conclusions. Duration of incubation is a generic feature among pleurobemines and lampsilines (see *Popenaias* and *Obliquaria,* respectively, in Heard & Guckert, 1970), and some of the lamellidentine groups may yet be shown to be of the short-term habit.

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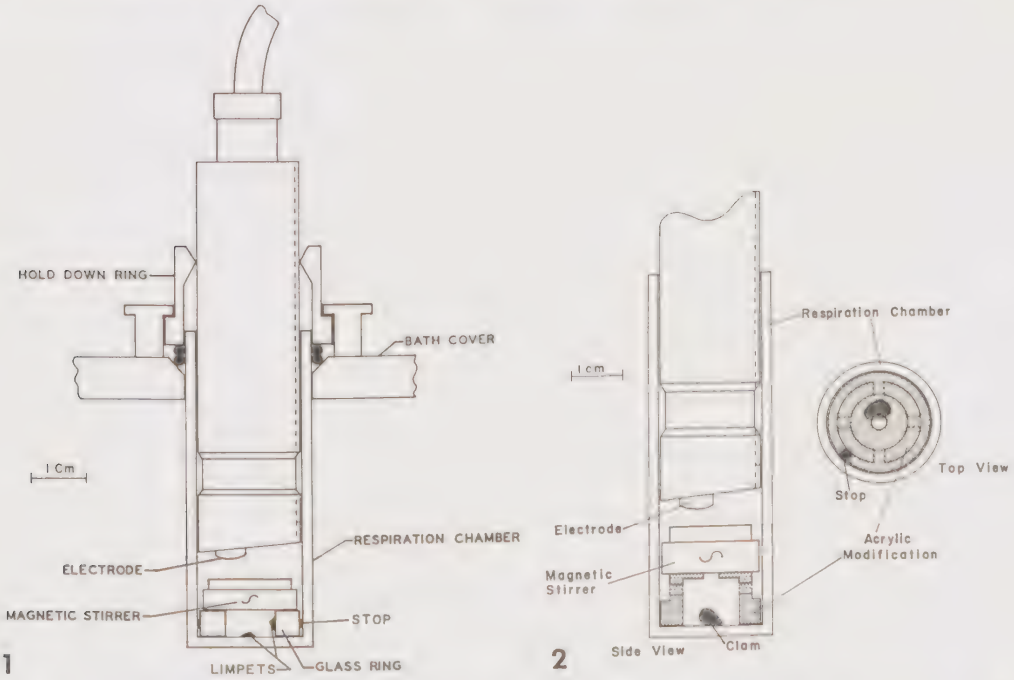
RESPIRATION CHAMBERS FOR MEASURING OXYGEN CONSUMPTION OF SMALL AQUATIC MOLLUSCS WITH CLARK-TYPE POLAROGRAPHIC ELECTRODES. – Clark-type polarographic oxygen electrodes (Clark, 1956; YSI Model 5331), respiration chambers (YSI Model 5213), water bath assembly (YSI Model 5301) and oxygen monitor (YSI Model 53) were purchased from the Yellow Springs Instrument Company, Yellow Springs, Ohio. The equipment is designed for measuring oxygen consumption rates on tissue homogenates or suspensions of cellular cultures. Modifications of respiration chambers are described for adapting the basic YSI system for taking measurements on small whole snails and clams.

Fig. 1 shows a chamber modification made by taking slices from a thick-walled glass tube (a similar ring can be made from plastic tubing). Suitable non-toxic "stops" made of surgical polyethylene tubing or of tygon tubing are placed between the glass ring and the chamber wall to prevent spinning of the unit. This chamber modification has been used for oxygen consumption measurements on the ancylid limpets *Ferrissia rivularis* (Say) (Burky, 1969, 1970, 1971) and *Laevapex fuscus* (C.B. Adams) (McMahon, 1973). The spinning magnet above the limpets allows mixing of the water between the area of the limpets and the area of the electrode for reliable readings. This type of chamber modification is satisfactory for animals with a large sucker foot and probably simulates the current conditions of streams and rivers where some populations of *F. rivularis* and *L. fuscus* are found. However, the modification in Fig. 1 is unsatisfactory for obtaining measurements on small clams and snails which are not adapted for habitats in swift currents. Fig. 2 illustrates a chamber modification which is turned from solid acrylic plastic. A "stop" between the acrylic modification and the chamber wall prevents spinning of the unit, and the 5 small holes in the plastic allow adequate mixing of water between the areas of the electrode and of the animals without disruptive



FIGS. 1, 2. Respiration chambers and oxygen electrodes modified for measuring respiration rates. These diagrams are partly based on a figure in the instruction manual of the Yellow Springs Instrument Company for the YSI Model 53, Biological Oxygen Monitor. FIG. 1. Glass ring modification. FIG. 2. Acrylic chamber modification.

turbulence. This author has used the modification in Fig. 2 for measurements of oxygen consumption on the sphaeriid clam *Pisidium walkeri* Sterki (Burky and Burky, 1976). The modification in Fig. 2 could also be used to take measurements on a variety of both freshwater and marine molluscs, as well as on other small aquatic animals of other phyla.

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THE USE OF MUCOUS TRAILS IN GASTROPOD ORIENTATION STUDIES.—An animal's movements are often studied to determine its responsiveness to directional stimuli. It is sometimes sufficient only to know the direction of an animal relative to its release point after a specific time has elapsed or a resultant distance has been travelled. Regardless of the criterion used, the animal's movements may be estimated by a resultant vector (Fig. 1), and subsequent analysis may be based only on a series of these vectors from multiple releases. However, researchers are often interested in the actual path taken by an animal travelling between 2 points. Paths may be recorded by direct observation, automatic techniques, or, in some species, individuals may themselves produce a record of their movements (e.g., the mucous trails of many mollusks and turbellarians). Herein I review past procedures, and present new ones, for the detection, recording, analysis and removal of mucous trails in experimental studies on the orientation of gastropod mollusks.

Detection of trails. In typical experiments, a snail is permitted to crawl on an artificial surface (hereafter, the surface) which is subsequently treated to render the mucous trail more visible for analysis. Ullyott's (1936a) method of exposing the surface to a suspension of talc, a substance adhering to the mucous trail and making it clearly visible after a water rinse, has been used successfully by other researchers, sometimes with slight modifications (Morton, 1960 (with a bivalve); Yasuraoka, 1967; Boyle,

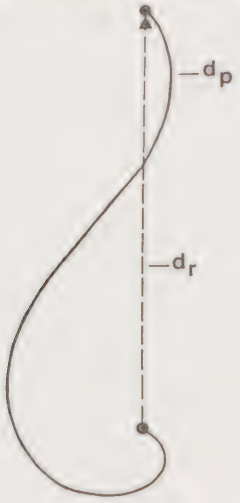

FIG. 1. The direction of the resultant vector (dashed line) for a path (solid line) in the mean direction taken by the animal. The length of this vector (d_r) divided by the actual path length (d_p) provides an index of directness (d) for the path.

1972 (with a chiton); Gendron, 1977). Other workers have placed ink powder (Bower, 1962) or a chemical dye (Irwin, 1966) in contact with snails to immediately produce visible trails. These latter methods seem less desirable since the effects of ink powder or dye on snail behavior are unknown.

I have found a less complicated technique useful for detecting gastropod mucous trails. A non-porous transparent material (e.g., sheet glass or plastic) is used for the surface to facilitate subsequent recording and removal of mucous trails. For tests conducted in air, a light mist of clean water sprayed on the surface results in water droplets adhering in a distinct pattern to the mucous trail. For tests conducted in water, placing the surface in the air at a slight tilt to permit most of the water to run off results in a water film adhering to the mucous trail. In either case, the mucous trail can be clearly seen. The above procedure is successful with *Littorina irrorata* (Littorinidae), *Deroceras laeve* (Limacidae), *Melongena corona* (Melongenidae) and *Nassarius vibex* (Nassaridae).

Recording trails. After the mucous trail is made visible, a permanent record of the snail's path is usually required. A primary method has been drawing or tracing by hand, sometimes with the aid of a grid system (Newell, 1958; Morton, 1960; Charles, 1961; Yasuraoka, 1967; Warburton, 1973).

I have found a fast and accurate technique useful for permanently recording mucous trails left on a transparent surface. The surface is turned over and the path is traced on that side of the surface opposite the mucous trail with a pen containing a specific type of ink. Water should be able to dilute the ink when wet to facilitate cleaning the surface afterwards, and the ink should adhere poorly to the surface, coalescing instead into numerous minute droplets. Both India ink (e.g., "Higgins Black Magic") and some felt-tip pens (e.g., some colors of "Flair" pens) work well on glass and "Plexiglas", although the latter inks may not be waterproof. The ink-traced trail is then pressed onto a piece of paper, producing a positive image of the snail's path. If a non-waterproof ink is used, the path image can then be retraced with a waterproof ink or pencil.

Analysis of paths. The mean direction taken by an animal is the direction from the starting point to the end point (i.e., the direction of the resultant vector in Fig. 1), a fact determinable without knowledge of the path actually taken. Researchers typically analyze the actual path to learn whether an animal was oriented (i.e., followed a non-random path). Batschelet (1972) indicated that present day statistics cannot determine whether a particular path is oriented, but offered a "modest approach" to such statistical analysis.

Often encountered extensions of the basic question "Was the animal oriented?" are, "Was the animal more oriented during one part of its path than another?" and, "Were animals in one situation more oriented than animals in another?" I have found a simple index for the degree of directed orientation which is amenable to analysis by established statistical procedures, and is thus useful in answering these latter questions (see Hamilton, 1976). It is obtained by measuring the path length with a curvimeter (e.g., a mechanical map reader) and the resultant distance travelled with a straight rule. The index of directness (d) for the path is then computed as follows (Notations as in Fig. 1):

$$d = \frac{d_r}{d_p}, \text{ where } d_r = \text{resultant distance travelled; } d_p = \text{path length}$$

The index will always take on values between 0.0 and 1.0, being low for circuitous paths and high for straighter paths. Those familiar with statistical tests for circular distributions will note that this index of directness (d) would be equivalent to the length of the mean vector (r) in the Rayleigh Test (Batschelet, 1972) if the assumption of independence of the infinitesimally small component vectors comprising the actual path were met. The fact that the direction of each component vector somewhat depends on the direction of each preceeding component vector is apparently the main obstacle to statistically determining if a path is oriented (Batschelet, 1972). With this quantitative measure for the degree of directed orientation (directness) of a path or portions thereof, statistical comparisons between or among groups can be conducted. Non-parametric methods should be employed since 'd' is rarely distributed normally. This analytical procedure is less complicated than the r.c.d. (rate of change of direction) measure Ullyott (1936b) developed to analyze paths of animals exhibiting undirected responses (kineses).

Yasuraoka (1967) noted that paths of light-adapted *Oncomelania nosophora* (Hydrobiidae) placed in a dark aquarium were circuitous immediately after the light was turned off, but became much straighter after a short time. He suggested that the former behavior resulted from a shadow reaction, and the latter from eventual dark adaptation of the snail's eye. However, many species (including non-mollusks) initially exhibit circuitous movements upon release regardless of experimental conditions, and it can be concluded that each animal is merely "getting its bearings". Gastropod orientation studies that did not subject experimental animals to marked changes in light intensity also reported initial circuitous paths followed by straighter paths, under some conditions (e.g., Warburton, 1973; Hamilton, 1976). For example, Warburton distinguished between an early "adjustment component" and the eventual "PRB" (primary route bearing) taken by *Nerita plicata* (Neritidae).

Because snails' paths are often initially circuitous, it is desirable to minimize or eliminate the influence of this portion of the response on the measure of orientation eventually assumed by an animal. Some researchers (e.g., Warburton, 1973) have used only the mean direction taken after each snail's path was qualitatively judged to straighten. This procedure risks introducing personal bias into the data, but has

the advantage of accommodating variability in the rapidity with which individuals assume a straight path. An alternate method that I have found useful (Hamilton, 1976) involves determining a criterion distance or time beyond which the path becomes straight (based on qualitative observations during preliminary tests), and by then measuring the mean direction from the criterion to end points on the path. For example, the mean direction eventually taken by the snail whose path is shown in Fig. 2 would be measured upon reaching a criterion distance from the release point (distance from Point A to Point B), and hence would be the direction from Point B to Point C (dashed line). This method eliminates the potential effect of personal bias on the data, but may not accommodate individual variability if the preselected criterion value is not sufficiently large.

Probably the best method for determining when a path straightens would be to compute the index of directness for numerous increments of the path, and to declare the path "straight" when a value, or the mean of several consecutive values, exceeds a specified number. This method would accommodate individual variability and eliminate the potential effect of personal bias on the data, but would also be more time-consuming unless accomplished by computer.

Removal of mucus. Cook & Cook (1975) reviewed numerous studies documenting the ability of gastropods to follow intraspecific mucous trails, and of some species to detect the trail's polarity. Hence, it should be assumed that this capability is universal among gastropods when designing experiments, in the absence of data to the contrary for each species (Wells & Buckley, 1972).

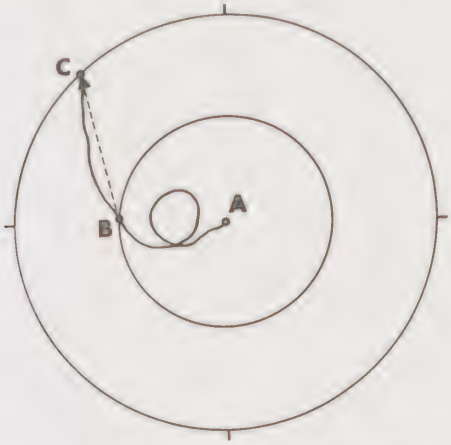

FIG. 2. By measuring the mean direction taken by an animal after it reaches a criterion distance (B) from its release point (A), the influence of any initial randomly oriented movement upon release is minimized in the measure of orientation eventually assumed by the animal.

Some past researchers (e.g., Bovbjerg, 1965) have purportedly overcome the difficulty of rapidly acquiring data on slowly moving gastropods by simultaneously releasing more than one snail in an experimental arena, while making the unstated and potentially inaccurate assumption of independence. Although this procedure may not necessarily lead to erroneous conclusions, the data and any statistical inference are at least partially compromised because the number of independent responses is unknown. Other researchers either have failed to mention procedures for eliminating mucous trails from experimental surfaces used repeatedly, thus raising the possibility that trails were totally ignored (e.g., Evans, 1961), or have spread the mucus uniformly over the surface between trials, thus eliminating only directional information (e.g., Hermann, 1968). While the latter procedure is preferable to the former, some aspects of a snail's behavior (e.g., rate of locomotion) are probably modified by the presence of conspecific mucus.

The above weaknesses should make clear the need for testing snails singly in experiments, and for completely removing mucus from the surface between trials. A simple washing of a "Plexiglas" surface in

clean water with paper towels, followed by hand-drying with additional towels, is adequate for mucous trails left by *Littorina irrorata*. However, Wells & Buckley (1972) note that mucous trails of some gastropods (e.g., *Physa acuta*, Physidae) are more difficult to remove. Hence, experiments involving mazes (e.g., Wells & Buckley, 1972) should be accompanied by a demonstration of the effectiveness of the method for removing mucous trails. Experiments involving an arena with stimuli in fixed positions (e.g., Hamilton, 1976; Gendron, 1977) should include a method for randomizing the direction of any residual mucus left after cleaning, such as rotation of the surface. A disposable surface may also be practical in some situations. The mucus-specific dyes Alcian blue (Cook, 1971) and toluidine blue are useful in checking for residual mucus of several species.

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AN INTRODUCTION OF *ACHATINA FULICA* TO AUSTRALIA.[1] – On 23 April 1977 the Australian Museum received a parcel containing 1 live, mature specimen of *Achatina fulica* Bowditch (Fig. 1) from near Cairns in northern Queensland, sent for identification by Mr. Clyde Coleman of Herberton. Immediate contact was made with both Federal and State quarantine officers, and within an hour investigations were being carried out in the Cairns area as to possible spread of the snail. Several generations of *A. fulica* were found at the original site, a suburban garden in the small sugar town of Gordonvale, about 16 km south of Cairns. All of the snails were hand-collected and destroyed. However, more collecting that night showed that a large hatching had recently occurred, since hundreds of juveniles, too small and too numerous to hand-collect, were found. A large tarpaulin was spread over the area and methyl bromide gas pumped under it, a technique that apparently was successful in killing all specimens.

FIG. 1. Specimen of *Achatina fulica* from Gordonvale, northern Queensland, Australia, sent to the Australian Museum for identification. Photograph by Greg Millen, Australian Museum.

In the next few weeks, thorough hand-collecting, the disbursing of metaldehyde pellets, and wide, local publicity by the news media and schools, resulted in more specimens being collected, showing a spread of *Achatina fulica* for several hundred metres from the epicentre. However, few snails are being found as of this date (September 1977) and it appears that the infestation now may be controlled and most of the snails destroyed. Nevertheless, some years of continued monitoring is required, especially since the latest surveillance occurred during the dry season; there could possibly be a resurgance of *A. fulica* during the next wet season (November-March). Fortunately, the town of Gordonvale is completely surrounded by sugar cane fields which are burnt before harvesting, and this fact may have been the main factor in preventing this potentially severe pest from spreading into the lush and extensive rainforests in the vicinity. Mead (1961) reported that while *Achatina fulica* has not been recorded as being a pest of sugar cane, it can cause extensive damage to young crops through sheer weight of numbers climbing up the plants and breaking them. In Australia, possibly the extensive and well-managed crops around Gordonvale have been an efficient barrier to the spread of *A. fulica*.

It is puzzling to know how the snail first got to Gordonvale, several kilometres inland from the coast. Cairns, with a shipping port and an international airport, is about 16 km away, and no specimens have been found there. However, the investigations at Gordonvale indicate that it is probable that *Achatina fulica* has been in the epicentre for 2 years, so that question is mainly academic. Of more immediate concern to quarantine officers in Cairns is control methodology.

Experience gained from control attempts in Hawaii indicate that on no account should biological control methods using carnivorous snails such as *Euglandina rosea* (from Florida) and *Gonaxis quadralateralis* (from Kenya) be used. Where these 2 predators have been introduced they have eliminated many native species and seem to have made no appreciable impact on *Achatina fulica*. Chemical methods and hand-picking seem to offer the only hope.

Currently known distribution, outside of its native East Africa, includes much of the Indian subcontinent, including Sri Lanka; the Indo-Malayan Archipelago, including Borneo; much of coastal Papua New Guinea; the Islands of New Britain and New Ireland and others in the vicinity; the Philippines; Bonin Islands; various of the Marianas (Pagan, Saipan, Tinian, Rota, Agiguan and Guam); Truk and Papau in

the Carolines; New Hebrides, New Caledonia (both recent introductions); Tahiti and probably other islands in the Society Group; and the Hawaiian Islands.(2) It was first introduced to India about 1856 by Benson (Godwin-Austen, 1908) and later introductions were to Formosa and Japan, and then elsewhere. A recent introduction to Miami, Florida, on the North American mainland, apparently now has been successfully eradicated – at a cost of over US$ 300,000 (Mead, 1977).

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(2) NOTE: The author would very much appreciate information about additional distributional records of *Achatina fulica* in order to inform quarantine officials, so that they know which vessels and air planes arriving in Australia need to be especially thoroughly searched.

A NEW FRESHWATER SNAIL (BASOMMATOPHORA: PLANORBIDAE) FROM AUSTRALIA, *PLESIOPHYSA JOHNI*.(1) – The most common freshwater mollusks in Australia are non-planate planorbids, i.e., their shells are not the discoidal type from which the family Planorbidae gets its name. This group of snails has been greatly over-named, prompting Hedley & Musson as early as 1892 to observe that "upon few genera has synonymy, that curse of Babel upon science, fallen heavier than upon the Australian *Bulinus* [= non-planate planorbids]." However, at least one species of this group has not been discovered previously, and the purpose of the current paper is to describe this new species. By its small, sinistral, neritiform shell, *Plesiophysa johni*, described here, is readily distinct from any other known planorbid. No doubt the new species had not been found before because it has a very limited distribution and it comes from a remote area of Australia that has been little collected.

Plesiophysa johni, nov. sp. (Fig. 1a). Description. *Shell*. The shell is small, thin, sinistral, with up to 2 rapidly increasing whorls, the last (body) whorl being disproportionately large, giving the shell a neritiform appearance. The suture is deeply impressed. The aperture is oval, its length being nearly equal to the shell length. The peristome is continuous, even on young shells, and is bordered by a thin ring of periostracum, which continues slightly beyond the edge of the calcium carbonate part of the shell. The columellar margin is reflected and slightly curved, without a trace of a columellar fold or a terminal truncation. The umbilicus is a narrow, deep perforation. The spire is very small and low, extending slightly above the aperture in apertural view, and is badly eroded in older specimens. The periostracum is dull and is a shade of buff (approximately light buff to cinnamon-buff, by Ridgeway's (1912) color standards and nomenclature).

The type lot contained the holotype and 12 paratype shells (and broken parts of several additional shells). Two of the paratypes are in the Western Australian Museum and 2 are in The University of Michigan's Museum of Zoology. The holotype and the other paratypes are in the Australian Museum, Sydney.

FIG. 1. a, Apertural and dorsal views of the holotype shell of *Plesiophysa johni* (scale = 1 mm). b, radular teeth of *P. johni* (c = central tooth; 1 = 1st lateral; 8 = 8th lateral; scale = 10 μ).

Dimensions. Measurements of 4 specimens of *Plesiophysa johni* are as follows: (1) length 3.1 mm, width 3.2 mm (Holotype); (2) length 3.3 mm, width 3.5 mm (Paratype); (3) length 3.2 mm, width 3.4 mm (Paratype); (4) length 3.1 mm, width 3.4 mm (Paratype).

Animal. Several dried specimens were softened with potassium hydroxide and from these a few details of the external appearance of the animal of *Plesiophysa johni* could be discerned. The foot is proportionately very large, presumably an adaptation for adhering to the substratum when flooded during the wet season. The spiral form of the body comprises only one volution or whorl, the upper (posterior) visceral part of the coil being very small. The mantle is intensely pigmented with black, except for its terminal (apertural) border where pigment is absent, and on a small area of the right ventral visceral part of the mantle, i.e., on the ventral columellar side of the upper (beginning) body whorl. The head and sides of the foot are moderately pigmented, and the ventral surface of the foot seems to lack pigment.

Radula. The radula (Fig. 1b) of 2 dried specimens were cleared from surrounding tissues by potassium hydroxide, mounted in water on a microscope slide and viewed with bright field and phase contrast microscopy. Each rhachidian tooth of the single central vertical row has 5 cusps: a prominent central cusp or mesocone, flanked on each side by 2 ectocones. The ectocones closest to the mesocone are larger than the 2 outer ectocones on each side. The endocones of the lateral teeth are large, becoming excessively developed from the 2nd lateral out to the marginals. The mesocones of the 1st lateral teeth are very small, and from the 2nd-10th lateral they tend to be masked by the ectocones. The transition in cusp form from lateral teeth to marginal teeth is not abrupt. The general radula formula is 10-10-1-10-10,

or 20-1-20 if the transition between laterals and marginals should not be considered abrupt enough to distinguish the 2 types.

Type locality. Pool in dry watercourse running north 1 mile to join unnamed creek. The latter creek runs east 1 mile to join left bank of Isdell River at a sharp bend near the bottom of Isdell Gorge about 3 miles up from the mouth of Isdell River in Walcott Inlet, northwestern Australia. Collected on 28 August 1943 by an unspecified collector.

Although the exact type of habitat in which *Plesiophysa johni* occurs is not yet known, its neritiform shell would indicate that it spends much of its time in turbulent water. Since its locality is in a stream, it probably lives during the wet season either in swift water in the stream proper, or in water falls.

Generic placement. The shell of *Plesiophysa johni* is readily distinct from that of any of the other non-planate Planorbidae described for Australia. Although its anatomy is not yet known, the characteristics of the central radular tooth of *P. (B.) johni* point to a relationship with the Neotropical genus *Plesiophysa* Fischer 1883, the only planorbid genus without bicuspid central teeth. Because *P. johni* shares the 5-cuspid rhachidian tooth with *Plesiophysa* (cf. Bland & Binney, 1873; Fischer, 1883; Bequaert & Clench, 1939; Hubendick, 1955), this new Australian species is provisionally placed in that genus. However, *P. johni* is distinct from the Neotropical species of *Plesiophysa* by its neritiform shell shape, small size, and in particular, the arrangement of the cusps on the lateral teeth; these characters isolate it in a new subgenus or section, to be called *Bayardella*.

Comparisons. The shell sculpture of *Plesiophysa johni* is readily distinct from nearly all other Planorbidae, but it is similar in many respects to the higher spired Australian *Camptoceras cosmeta* (Iredale 1944), a species originally placed by Iredale in *Glyptomoda* Iredale 1943 (type species: *Physa (Ameria) aliciae* Reeve, 1862), a generic name considered by Zilch (1959) to be a synonym of "?*Glyptaphysa* Crosse 1872." Like *P. johni, C. cosmeta* also has an oval aperture and complete periostome. However, "*G.*" *cosmeta* has bicuspid rhachidian teeth, and its accessory praeputial organ clearly indicates its relationship to *Camptoceras* Benson 1843 (type species: *Camptoceras terebra* Benson 1843).

The shells of *"Ameria" leopoldi* Dupuis 1931 resemble *Plesiophysa johni* somewhat, but Dupuis described the periostracum of *"A." leopoldi* as being hirsute and the spire as being completely enveloped by the last whorl. *"Ameria" leopoldi exserta* Dupuis 1931 is high-spired. The peristome of neither is complete and separated from the parietal wall. The anatomy of *A. leopoldi* and its subspecies have not been studied. Both were described from Lake Angi-Gita in the Arfak Mountains, Dutch New Guinea (West Irian).

In summary, *Plesiophysa johni* differs from all other Australian Planorbidae by its neritiform shell (a feature which is unique not only for Australia, but for planorbids in general), and by its 5-cuspid rhachidian teeth (a character which it shares in the Planorbidae only with the Neotropical *Plesiophysa*). This new species and subgenus is named in honor of my late son, John Bayard Burch, Jr.

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NEWS AND ANNOUNCEMENTS

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SIXTH EUROPEAN MALACOLOGICAL CONGRESS. – The Sixth European Malacological Congress was held in Amsterdam, The Netherlands, from 15 to 20 August 1977. The contributions to the Congress by members included twelve invited papers, a larger number of contributed papers, and various demonstrations presented as illustrated posters. The Proceedings of the Sixth European Malacological Congress will be published in a forthcoming issue of *Malacologia*. For additional information regarding the Sixth Congress, write to Dr. A.C. van Bruggen, Department of Systematic Zoology of the University, c/o Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, The Netherlands.

SEVENTH EUROPEAN MALACOLOGICAL CONGRESS. – The Seventh European Malacological Congress will be held in France in 1980. The new president is Mr. Jean M. Gaillard, Laboratoire de Biologie des Invertébrés marins et de Malacologie, Muséum National d'Histoire Naturelle, 55 Rue de Buffon, Paris 75005, France.

UNITAS MALACOLOGICA. – The following information has been received from Mr. Jean M. Gaillard, President of the Unitas Malacologica Europaea. "Dear Colleagues: At the recent General Assembly of Unitas Malacologica Europaea it was decided that the next Congress should be held in France in 1980 and I was elected President. This is both a great honour and an enormous responsibility and I thank my European colleagues for this token of their trust. However, the organisation of the Seventh Malacological Congress will be the joint responsibility of many French malacologists. We hope you will attend the Congress and present the results of your recent research. For our part we will endeavour to provide the conditions to make your stay a rewarding one. Attention will be given to the provision of adequate facilities for holding informal meetings outside the scope of the programme. We hope that each of you will appreciate and enjoy the advantages of such specialized meetings.

No doubt some of you will have ideas concerning the organisation of the meetings, accommodation and trips, whether scientific or purely for pleasure. We would be pleased to receive suggestions, and I thank you in anticipation.

Previously, our non-European colleagues were only corresponding members of UME with very limited rights. The General Assembly in Amsterdam modified the rules of the Union and the organisation is now open to all scientists interested in molluscs on a world-wide basis. Next year the name will be changed to Unitas Malacologica. This was an extremely important decision as it increased the possibilities of contact between malacologists from a widely diverse range of countries." – Jean M. Gaillard, Laboratoire de Biologie des Invertébrés marins et de Malacologie, Muséum National d'Histoire Naturelle, 55 Rue de Buffon, Paris 75005, France.

MOLLUSCICIDE SECTION OF THE 1977 INTERNATIONAL CONTROLLED RELEASE PESTICIDE SYMPOSIUM. – Papers on the development, evaluation and field usage of controlled release molluscicides and schistolarvicides were presented to the Molluscicide Section of the 1977 International Controlled Release Pesticide Symposium held in Corvallis, Oregon, U.S.A., during the week of 21 August 1977. The proceedings of the Symposium will be published in the near future. For further information write to Dr. Nate Cardarelli, Environmental Management Laboratory, University of Akron, Akron, Ohio 44325, U.S.A.

CORBICULA SYMPOSIUM. – The First International *Corbicula* Symposium, sponsored by the Texas Christian University Research Foundation, was held in Irving, Texas, on the 13th, 14th and 15th of October 1977. Contributors to the symposium included J.C. Britton, Larry Eng, J.S. Mattice, Brian Morton, C.E. Murphy, Leo W. Newland, James Sickel and Ralph Sinclair. For information regarding the symposium, write to Dr. Joseph Britton, Department of Biology, Texas Christian University, Fort Worth, Texas 76129, U.S.A.

STANFORD UNIVERSITY COLLECTIONS TRANSFERRED TO THE CALIFORNIA ACADEMY OF SCIENCES. – The molluscan shell collection, the type specimen collection, and a major part of the invertebrate fossil collection of the Department of Geology, Stanford University, have been transferred on indefinite loan to the Department of Geology, California Academy of Sciences. All enquiries regarding these Stanford University collections should be directed to the California Academy of Sciences. The combined Academy and Stanford collections are now available for study. The shell and fossil collections are housed separately, and both collections have work space and other facilities for visitors.

The combined California Academy of Sciences-University of Stanford shell collection, containing an estimated one million specimens, is of world-wide scope, but it is especially rich in marine species from the eastern Pacific and land snails from western North America. The fossils transferred from Stanford University to the California Academy of Sciences include the Cenozoic stratigraphic collection and the systematic collection of fossil cephalopods and echinoids. The combined Academy-Stanford fossil collection contains about one million specimens (mostly mollusks), principally from Cenozoic and Late Mesozoic rocks of the Pacific Coast of North America (Alaska to Mexico). The combined Academy-Stanford type collection, housed in a separate room, contains several thousand specimens, including primary and secondary types of living mollusks, and fossil invertebrates (mostly mollusks), vertebrates and plants. – Peter U. Rodda, California Academy of Sciences, San Francisco, California 94118, U.S.A.

SUMMER COURSE IN MALACOLOGY OFFERED BY THE UNIVERSITY OF MICHIGAN. - The Division of Biologicsl Sciences of The University of Michigan will offer a course in "Malacology" (Zoology 438) during the 1978 summer half-term (June 28 - August 15). This course will be open to both undergraduate and graduate students. Registration will take place on June 26 and 27, 1978. (The period for early registration is April 3-18.) For further information regarding registration, write to Admissions Office, 1220 Student Activities Building, The University of Michigan, Ann Arbor, Michigan 48109. For information on course content, write to Dr. J.B. Burch, Department of Ecology and Evolutionary Biology, Division of Biological Sciences, The University of Michigan 48109.

NEW MOLLUSK CURATOR AT THE UNIVERSITY OF MICHIGAN. – Dr. Alex Tompa has been appointed to fill the vacancy created by the retirement of Henry van der Schalie, and will join Dr. J.B. Burch as the second Curator in the Museum of Zoology's Mollusk Division. Dr. Tompa will also have a part-time appointment as Assistant Professor in the Department of Ecology and Evolutionary Biology, Division of Biological Sciences. Dr. Tompa came to The University of Michigan from Duke University.

PUBLICATIONS ON NORTH AMERICAN FRESHWATER SNAILS. – Freshwater snails form an important part of the biota of North American streams and lakes, and as more attention is directed to the disappearing faunas of our freshwaters, especially in regard to conservation, environmental impact statements, pollution, etc., the specific identification of our freshwater snails becomes of increasing concern. Satisfactory manuals and identification guides exist for very few regions of North America; most publications of this kind are both out of date and out of print. There is no adequate, up-to-date manual for the entire North American freshwater snail fauna. To help remedy this, three publications are currently in preparation. The first two of these are 1) an "Outline of the classification of North American freshwater gastropods," to appear in a forthcoming issue of the *Journal de Conchyliologie*, and 2) "A synopsis of the classification of the freshwater gastropods (snails and limpets) of North America (north of Mexico)." The latter is scheduled for publication in late 1978 by Malacological Publications, P.O. Box 194, Hamburg, Michigan 48189, U.S.A. These two publications will be followed by a fully illustrated manual on freshwater snails to be published in 1979 by the Environmental Monitoring and Support Laboratory, Environmental Protection Agency, Cincinnati, Ohio. For further details, contact Dr. J.B. Burch, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

INDEX TO THE *ANNUAL REPORTS* OF THE AMERICAN MALACOLOGICAL UNION, INC. – An index for the years 1934-74 to *The American Malacological Union, Inc., Annual Reports* (now called *The American Malacological Union, Inc., Bulletin*) has been prepared by Mrs. Margaret Teskey, Honorary Life Member and former Secretary of the American Malacological Union. The index appears in 3 parts: (1) a chronological listing of the dates, places and chairmen of the annual meetings, including those of the Pacific Division, (2) an author index wherein titles appear verbatim in chronological order, and (3) a reference index in several parts. Here titles have been transposed to present subject matter in alphabetical order, at times cross-indexed under two or more headings.

The Index is available from the Treasurer of the American Malacological Union, Myra L. Taylor, 7602 McCullough, San Antonio, Texas 78216, U.S.A. The price is US$ 6.50 (postpaid).

JOURNAL ABBREVIATIONS FOR LITERATURE CITATIONS IN *MALACOLOGICAL REVIEW*. – Perhaps the most commonly recurring flaws that an editor must deal with in processing manuscripts occur in the cited bibliographic references. As an aid to its authors, and to the editors, *Malacological Review* published in 1971 (Vol. 4(1): 29-40) a list of "Abbreviated titles of scientific journals and place names to be used in literature citations in *Malacological Review*." These were compiled from "those [journals, other publications and place names] cited by authors in previous issues of *Malacological Review*, as well as many cited in our affiliated journal, *Malacologia*."

Beginning with Vol. 11 (1978), *Malacological Review* will follow the journal abbreviations as listed in the *List of serials with coden, title abbreviations, new, changed and ceased titles* published annually by the BioSciences Information Service of Biological Abstracts, 2100 Arch Street, Philadelphia, Pennsylvania 19103, U.S.A. These lists are much more comprehensive, and are readily available. Most abbreviations in the *List of serials* are the same as previously used by *Malacological Review*, but there will be a few changes such as Am. for Amer. (American), Annu. for Ann. (Annual), Aust. for Austr. (Australian), Contrib. for Contr. (Contributions), Invertebr. for Invert. (Invertebrate), Jpn. for Jap. (Japanese), Nat. for Natur. (Natural, Naturalist), Natl. for Natn. (National), Publ. for Publs. (Publications), and Rep. for Reps. (Reports). A few of the names are not abbreviated, e.g., Board, Health, Public, and World (World Health Organization is abbreviated W.H.O.).

Authors preparing manuscripts are requested to refer to the BioSciences Information Service *List of serials* when preparing their bibliographies for *Malacological Review*.

REQUEST FOR LITERATURE ON PLANORBIDAE. – Mr. Friedrich Wilhelm van der Wart, Karel Doormanlaan 72, Haarlem, The Netherlands, is working on the freshwater pulmonate snail family Planorbidae, and requests literature on these mollusks, especially articles after 1940 in which new planorbid taxa are described.

MISCELLANEA

* * * * *

A BRIEF HISTORY OF *JOURNAL DE CONCHYLIOLOGIE*

Until the mid-19th century, no periodical journal was exclusively dedicated to malacology. Until then, results of malacological research had been published as important books (the great classical works which are the basis of our actual science), or, if of lesser importance, they were published in nonspecialized zoological journals. Moreover, during this period there existed certain misunderstandings among the various branches of malacology.

S. Petit de la Saussaye (1789-1870) was the first to think of starting a periodical journal devoted entirely to mollusks and to gather together the research of the various specialists of the time. Born in Rouen (Normandy), Petit de la Saussaye travelled for several years before becoming a civil servant in the French Ministry of the Navy in Paris. He had sailed in the China Seas, the Sunda Isles and the West Indies. During these travels his interest in mollusks was awakened. When he stopped sailing he contacted his various friends for help. It was thus that he studied the shells collected by Admiral Cecille (then stationed in Tahiti) and by Captain Hanet-Clery, Commandant Guillain, etc.

Before 1850, Petit de la Saussaye had published a few descriptions of species in non-specialized journals, such as *Le Magasin de Zoologie*. But he realized that such publications could not bring much help to malacologists. For this reason he founded the *Journal de Conchyliologie* in 1850, the first periodical dedicated to the study of malacology. The first home of the *Journal* was at the address of Petit de la Saussaye: 19, rue des Mathurins, Paris.

Besides the original articles, which were the main part of the *Journal de Conchyliologie*, Petit de la Saussaye included from the first volume onwards such information that would be useful to malacologists, and also bibliographical abstracts, which were greatly appreciated and continued by his successors during the entire period of publication of the *Journal*.

At a time when the concept of "type specimens" was practically nonexistent, Petit de la Saussaye had the idea of building up a collection of types described and figured in the *Journal*. This collection evidently did not include all of the types, but did include a large number of them – those which authors donated to him and his successors. H. Crosse later bequeathed this collection to Henri Fischer, along with the ownership of the *Journal de Conchyliologie*. A repertory of this collection was published by E. Fischer-Piette in 1950 in Volume 90 of the *Journal*.

As soon as it appeared the *Journal de Conchyliologie* was very popular. Systematicians, anatomists and paleontologists all wished to publish their findings in it.

From the very beginning, the *Journal* was and has always remained a "non-profit" publication. This means that its budget had to be balanced with no benefits. In actual fact, such a formula can only lead to deficit, light if possible, but more serious in periods of troubled economy. Petit de la Saussaye seems to have been faced with this financial problem from the start.

The first 4 volumes of the *Journal de Conchyliologie* were published, respectively, in 1850, 1851, 1852 and 1853, containing articles by the most prominent specialists of that time. However, this brilliant beginning was followed by disappointment: Petit de la Saussaye suddenly decided to interrupt his work, discouraged by a minor incident started by a jealous author. The *Journal* was discontinued for nearly 3 years. Then it was edited once again in 1856 by 2 naturalists, Paul Fischer and A.C. Bernardi.

Paul Fischer was born in Paris in 1835; he finally gave up his medical career for the science of malacology. Bernardi originally came from Verona, Italy. He was an artist, a student of the Venice Academy of Arts, and had come to live in France about 1835. After this date he became interested in mollusks, and had gathered a good collection of the genus *Conus*. By their collaboration, Fischer and Bernardi were able to bring out a 5th volume of the *Journal de Conchyliologie*, issued on 22 July 1856. This volume contained, among other articles, the description by Fischer and Bernardi of a "living fossil," the famous

Pleurotomaria quoyana, which had been found on the Island of Marie-Galante (French West Indies). The publication of the *Journal* from then on continued regularly.

Unfortunately Bernardi became ill and his actual contribution to the editing of the *Journal* ceased in 1860. He died in 1863. In 1861, Hippolyte Crosse then accepted to share the directorship of the *Journal de Conchyliologie* with Paul Fischer.

Crosse (1826-1898) was a man of exceptional character. While carrying on his job as a solicitor, he had developed a great passion for malacology. He was extremely active in regard to the *Journal* and shared a perfect understanding with his friend Fischer. Having considerable private means financially, he generously contributed enough to keep the *Journal* operating at a time when finances were sadly lacking.

When Dr. P. Fischer died in 1893, his son Henri Fischer was already well known for his work on mollusks, and Crosse took him on immediately as his associate for the direction of the *Journal*. Crosse died in 1898, having bequeathed to Henri Fischer the ownership of the *Journal*. The home of the *Journal* was transferred from Crosse's residence to that of H. Fischer, who then obtained the collaboration of P. Dautzenberg and G. Dollfus.

When H. Fischer died prematurely in 1916, it seemed that the future of the *Journal* was to be short-lived owing to the circumstances of World War I. However, Madame H. Fischer decided to continue the publication. She had the help of Dautzenberg, Dollfus and E. Lamy, and later on, in 1927, of P.-H. Fischer and E. Fischer-Piette. In 1950, Madame Fischer was able to celebrate the centenary of the *Journal*. The apartment of Mr. and Mme. H. Fischer, 51 Boulevard St. Michel, Paris, was not only the headquarters of the *Journal* for more than 50 years, but was also a place where numerous malacologists from all over the world could meet. After the death of Madame Fischer (1954) the *Journal* was taken over by P.-H. Fischer and E. Fischer-Piette, and then by P.-H. Fischer alone, when the *Journal* moved to its present address, 18/55 Prince Albert Street, Mosman 2088, Australia.

The *Journal de Conchyliologie*, chronologically the first of the malacological journals, had, since its beginnings, an international trend which is convenient for the development of a science, and it attracted a great deal of interest among the foreign malacologists. For example, among the American malacologists, 3 (Gould, Jay and Wilson) were "abonnés-fondateurs," which means they were among the subscribers to the first volume (1850). For the following volumes during this early period, American authors and subscribers included names such as Isaac Lea, T. Bland, G.W. Tryon, W.G. Binney, W.H. Dall, Bryant Walker, A. Agassiz, H. A. Pilsbry and C.W. Johnson, to mention only a few.

Later, the international character of our *Journal* prevailed. Numerous articles were published in the original language of the authors. It was also the *Journal de Conchyliologie* which took the initiative in promoting international malacological congresses. A first malacological "Reunion," organized in Paris in 1935 by the *Journal*, was followed by congresses in different European countries. But in this respect the original idea of the directors of the *Journal* was not entirely realized. It should be, as we still hope, on a world-wide scale, by an organization which can arrange periodical meetings of all malacologists throughout the world. Should this be accomplished, the main efforts and aim of all the successive directors of the *Journal de Conchyliologie* would thus be accomplished.

P.-H. FISCHER

Director
Journal de Conchyliologie
18/55 Prince Albert Street
Mosman 2088, Australia

Malacological Review, 1977, 10: 87-88

OBITUARY

ALLYN G. SMITH

Allyn Goodwin Smith was born in Hartford, Connecticut, June 4, 1893 and died at his home in Berkeley, California, on August 18, 1976, after a brief illness. During his 83 years he led a full, rich life. He was a man of unusual ability, wide knowledge and extraordinary energy. Even in his last years, his step was quick, his handshake firm, and he had the appearance and bearing of a much younger man. He was always busy, but never too busy to stop and chat with a friend; and his friends were legion.

Allyn came with his parents to Redlands, California, while he was still in grade school, received his secondary education there and attended the University of California at Berkeley, from which he graduated in 1916 with the degree of Bachelor of Science in Electrical Engineering. He worked a year with the Southern California Edison Company, when his career was interrupted by World War I.

He served in the U.S. Army from 1917-20 as a radio operator, and as an observer on Army planes. He seldom referred to his Army service, but it was not uneventful. He once remarked to this writer, "Those were the days when one literally flew by the seat of his pants."

On his return from the Army, he married Katherine Isabel Tapscott and obtained a position with the University of California at Berkeley as Chairman of the Technical Department of University Extension. In 1925 he accepted an appointment with the Pacific Telephone and Telegraph Company as Administrative Superintendent of Personnel, a position he held until his retirement in 1954.

It may truthfully be said that he followed 2 careers, with equal success in each. He had been interested in natural history since boyhood and presently began collecting and identifying shells, first as a hobby, then as an expert who had gained wide recognition in malacology. He served as president of the Institute of Malacology, a Director and Vice-President of the California Malacozoological Society, President of the American Malacological Union, and was active in other organizations in this field.

He became a member of the California Academy of Sciences in 1936, a Life Member in 1943 and a Fellow in 1952. Identification of fossil shells being important to geologists, he was appointed a part-time Research Associate in Geology at the Academy in 1952, on recommendation of the late Dr. G Dallas Hanna, then head of the Department.

In 1954, Mr. Smith took an early retirement from the Telephone Company, in order to devote himself full-time to work at the Academy. From 1955 to 1960 he served as Resident Malacologist and as Assistant to the Director of the Academy. In 1960 he was appointed Associate Curator of the Department of Invertebrate Zoology, and in 1963 Chairman of the Department. He was a member of the Galapagos International Scientific Project of 1964, sponsored by the University of California.

After his "second retirement" in 1972, he divided his time between the Academy and working at home on scientific projects.

He is the author of numerous papers on mollusks, including "Amphineura" (in Moore's *Treatise on Invertebrate Paleontology*), "The Marine Mollusks and Brachiopods of Monterey Bay, California" (with Mackenzie Gordon, Jr.), and *Land Snails of the Galapagos.* His field of scientific work as listed in *American Men of Science* reads: "Classification, taxonomy, distribution and ecology of land, freshwater and marine Mollusca of the Pacific Coast of North America; Chitons, worldwide, recent and fossil."

Through the years of his affiliation with the Academy, he was a generous donor of malacological material to its collection, the total number of specimens certainly being well over 10,000. He contributed a valuable scientific collection of photographs of natural history

Allyn G. Smith, August 1961

subjects. Also, due in large part to his activities, the California Academy of Sciences Department of Invertebrate Zoology has become one of the major repositories for invertebrate research material in western North America. Under his dedicated direction a vital consolidation of valuable scientific collections from a multitude of sources was transferred to the Academy. This important contribution to zoological science will long endure.

Mr. Smith is survived by his wife, Isabel, 2 daughters, Leslie and Shirley, a son, Allyn G. Smith, Jr., 3 grandchildren, and 1 great-grandchild, Allyn G. Smith III.

ROBERT C. MILLER

MALACOLOGICAL REVIEW, P.O. Box 420, Whitmore Lake, Michigan 48189, U.S.A.

Malacological Review, 1977, 10: 89-90

OBITUARY

CAREL OCTAVIUS VAN REGTEREN ALTENA
1907-1976

Carel van Regteren Altena died suddenly just before Christmas, 1976, bringing to an end a very fruitful life in which he made many friends around the world.

Trained as a biologist at Amsterdam University, where he obtained his Ph.D. in 1937, he joined the Rijksmuseum van Natuurlijke Historie, Leiden, as entomologist in charge of the Lepidoptera in 1941. Altena had unofficially trained as a malacologist, partly under the guidance of Tera van Benthem Jutting, had worked previously on Tertiary fossils of Java, and museum malacology as a career attracted him to such a degree that he was prepared to wait until the then curator of mollusks, Dr. C. Bayer, retired. After his stint as an entomologist Altena assumed Dr. Bayer's position in 1952 and he himself officially retired on 1 January 1973. Emphasis is placed here on the word "officially," because he worked until the day before his sudden, although not unexpected, death. From 1968 he shared his curatorial duties with Dr. Edi Gittenberger, now in charge of the department. Altena's health became steadily worse in the course of the years and suffering must have been intense, although he never uttered a single complaint.

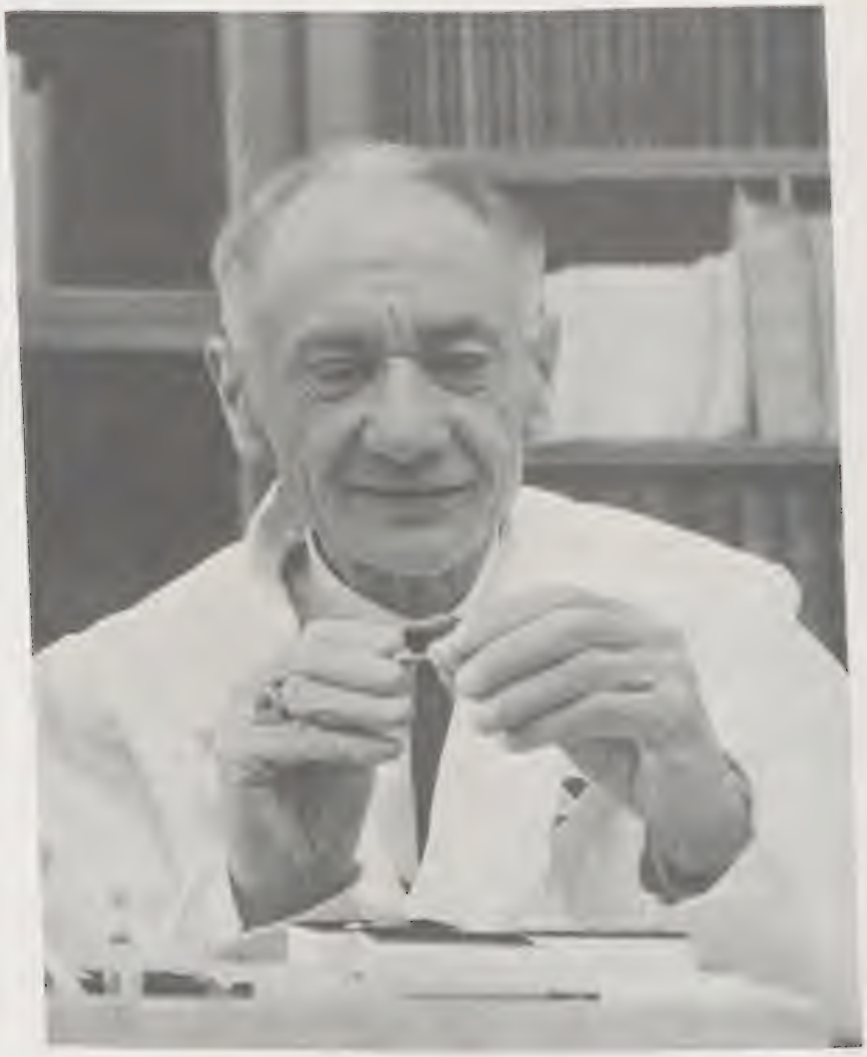
Until the 1960s, Altena mainly worked on European Tertiary, Quaternary and Recent mollusks. It is interesting to reflect upon the fact that he may have sought compensation for the purely conchological work on fossils in the study of land slugs in which field he became an acknowledged expert. In the years 1953-1977 he published a series of 25 "Notes on land slugs" (usually called "Notes sur les limaces" and sometimes also "Mitteilungen über Nacktschnecken") in addition to some other papers on these particular gastropods.

Since World War II much material from Dutch Guyana (=Surinam) accumulated at the Leiden museum and as part of a program of zoological exploration Altena travelled to Surinam in 1963 where he did extensive field work on both marine and non-marine mollusks. On his return trip he visited various museums in the United States in order to start work on the Surinam marine material. He made many American friends, some of whom he had met previously in Europe but with whom he was now able to spend more time, and he impressed them with his general knowledge and friendly, modest personality. After returning to Leiden, he maintained contact with them while writing up the results of his research which (apart from some smaller papers) appeared in print in 1969-1975 (3 papers on the marine mollusks in 1969, 1971 and 1975, and 2 on the terrestrial mollusks in 1974 and 1975).

Along with his career in the Leiden museum, he also made a name for himself as a paleontologist. In the period 1946-1976 he was curator of the geological, mineralogical and paleontological cabinet of Teyler's Museum in Haarlem. This is a very old (1780) but unfortunately little known museum of great importance and Altena made the most of his one day weekly at the Haarlem museum, where he mainly studied the rich fossil collections.

On the occasion of his 65th birthday the Dutch malacological society of which Altena was a founding member, treasurer (1934-1940) and president (1948-1967), dedicated the last issue of 1972 of *Basteria* to him as a tribute to all he did for the society and malacology in general. Since 1967 Altena had been an honorary member of the society, which he also served for a long time as senior editor of *Basteria*. The government recognized his services by appointing him an Officer in the Order of Orange-Nassau under the Queen's birthday honors in 1970.

Apart from the scientific achievements described above, Carel van Regteren Altena was a delightful person. No mean linguist (many of his papers were written in French, but he was equally at home with English and German), an accomplished musician and a gentleman



Dr. C. O. van Regteren Altena. Photo Chr. Hoorn, 1972.

in every sense of the word, he impressed all he met with his friendly approach and willingness to assist where he could. As a scientist he was not a fanatic; at heart he was a family man with a wide range of intellectual interests and a very complete personality.

His life and work were described in detail by van Benthem Jutting & van Bruggen (1972) on the occasion of his retirement from the Leiden museum; a more concise obituary was published by van Bruggen (1977). Both papers give lists of publications and new taxa: –BRUGGEN, A.C. van. 1977. In memoriam Dr. C.O. van Regteren Altena, 1907-1976. *Basteria*, 41: 1-6 (with portrait and English summary).–JUTTING, W.S.S. van Benthem & BRUGGEN, A.C. van. 1972. Carel Octavius van Regteren Altena, een schets van zijn leven en werken. *Basteria*, 36: 31-54 (with portrait and English summary).

A. C. van BRUGGEN

MALACOLOGICAL REVIEW, P.O. Box 420, Whitmore Lake, Michigan 48189, U.S.A.

BOOK REVIEWS

* * * * *

MOLLUSK FAUNA AND THE ZOOGEOGRAPHIC PARTITIONING OF CONTINENTAL WATERBODIES OF THE GLOBE. [In Russian.] Ya. I. Starobogatov. "Nauka", Leningrad Branch, Academy of Sciences of the U.S.S.R., Leningrad, U.S.S.R. 1970. 372p.

Starobogatov's monograph deals with the zoological zonation of inland waters of the 5 continents. For such a division into regions, the author used all available data on the habitats of living and fossil freshwater and brackish water bivalves and gastropods, which are among the most widely distributed groups of animals in lakes and rivers. It is noteworthy that the author considered not only the living malacofauna, but also fossil mollusks as well. A good preservation of the calcium carbonate shells of fossil mollusks has enabled the author to trace earlier periods of the development and spread of these organisms and gives a wider picture of their geographic distribution.

Being a prominent specialist on freshwater mollusks, Dr. Starobogatov considers many interesting and especially important problems of theoretical and practical importance.

The monograph consists of the introduction, 3 main chapters, a conclusion, and a supplement. The introduction to the monograph deals with principles and methods of the division of the world's freshwaters into biogeographic regions, and with the importance of such research. Starobogatov has rightly noted that up to the present time many investigations have been concerned with the zoogeographic division of the oceans and of the land, but little has been published on the zoogeographic division of inland waters. Many scientists have been sceptical about the possibility of dividing separate continental waterbodies into regions where endemism of hydrobionts seems to be very high. New data on contemporary and fossil freshwater organisms rejects such skeptical opinions completely, showing the wide migratory abilities of freshwater faunas. Only in large and ancient relict waterbodies is a high percentage of endemics observed as a rule. In the light of the new facts, Dr. Starobogatov shows the wide distribution of freshwater hydrobionts within the limits of certain geographic zones. It has been established that an active shift of mollusks goes on very slowly. But passive transportation by rivers and the essential repeated reconstruction of hydrographic systems during geological time, which took place with the changes of river drainages, favored rather quick and wide distribution of fauna throughout vast territories of the continents.

The 1st chapter is devoted to the distribution of freshwater and brackish water mollusks. This chapter is not only of zoogeographic but also of systematic importance, as the author generalizes here on the latest data affecting molluscan classification (and gives a wide synonymy). The well known systems of C. T. Simpson, F. Haas, H. Modell and many others cannot completely satisfy all systematists, and these systems have often complicated the identification of Recent and fossil faunas. Starobogatov has worked out a uniform and more satisfactory classification with well-grounded diagnoses. The systematic part of the monograph is supplied with maps showing the distribution of most of the families. However, much of the systematics of mollusks is still obscure, and therefore question marks are put before the names of some genera, indicating their problematic character.

The 2nd chapter deals with interesting problems of contemporary distribution of mollusks, the different periods in which organisms penetrated into continental waters, barriers to dispersal and ways of overcoming them, and the similarities and differences in the distributions of various freshwater groups. This chapter, unfortunately, is too brief and contains too few examples.

The main part of the book is the 3rd chapter, entitled "Zoogeographic Regions". This is a very important chapter for zoologists, hydrobiologists, paleontologists and zoogeographers.

In this part the author recognizes 9 zoogeographic regions for inalnd waters: the Palaearctic region, with 4 subregions and 34 provinces; the Ponto Caspian region, with 12 provinces; the Baikalian region, with 7 provinces; the Sino-Indian region, with 3 subregions and 32 provinces; the Ethiopian region, with 19 provinces; the Tanganyikan region, with 3 provinces; the Nearctic region, with 2 subregions and 19 provinces; the Neotropical region, with 2 subregions and 19 provinces; and the Australian region, with 14 provinces. The author gives the characteristic of each zoogeographic region, subregion and province, and the history of the mollusk fauna of every geographic subdivision. However, the division of very small zoogeographic provinces, some of which could be united, is questionable.

The text of the 3rd chapter is well supplied with maps. For example, a map of the Australian zoogeographic region shows possible ways of mollusk migrations; the Ethiopian region is supplied with a scheme of the Quaternary history of the hydrographic network of Africa. Paleographic maps of V. M. Sinitsyn and C. Schuchert show possible malacofaunal distributions on the globe. This chapter on the zoogeographic division of continental waterbodies into regions, despite several disputable parts, is undoubtedly interesting, because it contains the first analysis of the enormous literature dealing not only with malacological but also with general paleogeographic data.

At the end of the book the author has presented data on the systematics of freshwater and brackish water naiad bivalves and rissoacean gastropods. This part is not closely connected with the previous chapters, but, nevertheless, it is very important for systematic malacologists. Separation of new generic names of naiads based on literature revision is not quite indisputable, and sometimes is very doubtful.

Despite the critical remarks above, this monograph by Dr. Starobogatov is extremely interesting and deserves high praise. It can be said without exaggeration that this work is the first large generalization on the large and diverse freshwater and brackish water molluscan fauna, and presents an extensive and well-grounded zoogeographic classification. It is an excellent zoogeographic text book, which will be used by many zoologists, hydrobiologists, limnologists, paleontologists and paleogeographers.

G. G. MARTINSON

Academy of Sciences
of the U.S.S.R.
Leningrad, U.S.S.R.

MUREX SHELLS OF THE WORLD. An Illustrated Guide to the Muricidae. George E. Radwin & Anthony D'Attilio. Stanford University Press, Stanford, California. 1976. 284 p, 32 pls., 192 text-figures and 13 unnumbered figures. US$ 35.00.

Since the publication of Maxwell Smith's *An Illustrated Catalogue of Recent Species of the Rock Shell* (Tropical Laboratory, Lantana, Florida, 1939, ix + 83 p), shell collectors as well as specialists have been looking for the sort of book in which they will find information regarding both conchological identification and anatomical details of murex and rock shells. This volume deals with the conchological classification of murex shells, and readers will find a wealth of useful conchological information here.

An introductory chapter includes: the systematic position of the family Muricidae in the phylum, decisions and assumptions affecting classification, anatomical features, the radulae, feeding methods, reproduction, larval development, shell formation, purple dye, habitats, distribution, behavior, the fossil record and the methods of treatment. In general, this chapter briefly summerizes very well nearly all aspects of muricid biology known. However, some sections such as "decisions and assumptions affecting classification," "methods of treatment" and "characteristics of the five subfamilies" (Table 1), are apparently out of place. It would seem that they should be discussed in a subsequent chapter, under "Classification of the Muricidae."

The 2nd chapter, entitled "Family Muricidae," simply lists the names of subfamilies, genera and species. The basic shell characters which generally differentiate genera, such as the concise outlines given in Ruth H. Fair's "*The Murex Book*" (Sturgis Printing Co., Honolulu, 1976, xvi + 17-138 p), are perhaps more convincing and helpful to readers.

The series of 5 following chapters deals with 5 subfamilies of the authors, i.e., Muricinae, Ocenebrinae, Muricopsinae, Trophoninae and Typhinae. The arrangement of genera and species is alphabetical. Generic descriptions are largely the authors', except for the Subfamily Trophoninae. Among the 29 genera listed for the Subfamily Trophoninae, the original generic description was given only for the Genus *Xymenopsis*. The remaining 28 genera were, for the most part, not described, but in some cases, quotes or translations from other sources are included. The authors' extreme generic splitting results in many monotypic genera, which leads beginners into bewildering mass of generic terminology, which may eventually leave them helplessly lost, and not every malacologist will agree with the authors' taxonomic generic splitting.

The species descriptions contain partial synonymies, shell descriptions, distribution and sometimes geological records, and remarks. Shell descriptions are written consistently in order of size, spire, suture, body whorl, aperture, siphonal canal, sculpture and color for each species. In addition, the authors provide 32 excellent color plates and 122 black and white figures and line drawings of shells, protoconchs, opercula, microsculpture, intritacalices and cerata (labial teeth). These are of particular interest to both amateur collectors and specialists, and will be especially helpful to readers concerned with species identification.

Of the 70 radular figures, less than half of them are acceptable if based on critical standards. It would seem that the radulae were improperly or inconsistently mounted on their slides. This has resulted in irregularities in the drawing and stippling of the figures. Furthermore, neither the method of radular preparation nor the orientation and description of the radulae (except for the new species) were given. Unfortunately, the reader has to guess at an interpretation of the radular figures.

Chapters dealing with 2 species of "*Incertae Sedis*" and 38 species of "Uncertain Identity" repeat listings in the 2nd chapter. (Incidentally, more than half of the 38 taxa listed as of uncertain identity are more securely identified in Fair's "*The Murex Book*.")

An appendix proposing 16 new species seems out of place. These should have been treated in the main text in the context of their own taxonomic groups. The illustrated glossary and the data on the figured species are most useful. However, the radular terminology labelled on the drawing from the scanning electron micrograph (the dorsolateral view) in the glossary is irrelevant to the text-figures, which were viewed from either the dorsal or ventral aspects.

Topics which I would like to see, although they may be outside the scope of this book, are sound anatomical details of representative animals from each genus (or at least each subfamily), good radular figures and discussions, and some phylogenetic interpretation.

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THE BIOGEOGRAPHY AND NUMERICAL TAXONOMY OF THE OEGOPSID SQUID FAMILY OMMASTREPHIDAE IN THE PACIFIC OCEAN. Bulletin of the Scripps Institution of Oceanography, vol. 23. John H. Wormuth. University of California Press, Berkeley, California, U.S.A. 1976. 90 p. US$ 3.50.

The oceanic squid family Ommastrephidae, distributed throughout the world oceans, is represented by 23 recognized species, and, as such, is one of the most specious of oegopsid families. Ommastrephids are extremely abundant and occur in such huge numbers that extensive fisheries are supported. For example, about 500,000 metric tons of a single species, *Todarodes pacificus,* are landed each year from Japanese waters, while several ten-thousands of tons of 4-5 other species are captured in Atlantic, Mediterranean and Pacific waters. Furthermore, ommastrephids constitute significant portions of the diets of many marine mammals (e.g., toothed whales, seals), pelagic birds and large fishes. Several of the ommastrephid species (e.g., *Dosidicus gigas* and *Ommastrephes caroli*) attain quite a large size and are among the largest of squids.

While some of the species are distinctive and easily identified, most ommastrephids often have been identified by their localities of capture rather than by their morphological characteristics, a procedure that really isn't quite "fair." Besides, too frequently overlapping or sympatric closely related species occur, so the problem of identification becomes complicated. This is particularly true in the Atlantic Ocean where 3 species in each of 2 genera, *Illex* and *Ommastrephes,* are sympatric in parts of their ranges.

Such a taxonomic dilemma in the Pacific Ocean no longer exists because of the detailed study by John Wormuth, recently published as a Bulletin of the Scripps Institution of Oceanography. Prior to Wormuth's work the most comprehensive studies of ommastrephids were those of G. Pfeffer (1912, *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung,* Vol. II, Verlag von Lipsius & Tischer, Kiel-Leipzig, 815 p) and J. Steenstrup (1855-1898; translated in Volsoe, Knudsen & Rees, 1962, *Cephalopod Papers of Japetus Steenstrup,* Danish Science Press Ltd., Copenhagen, 330 p) when just over half the present number of species was known. Wormuth's effort, therefore, represents a much needed study. Based on the extensive collections of Scripps Institution, the work concentrates on the interspecific relationships and geographical distributions of Pacific Ocean species. In this approach, Wormuth is more concerned with the inter-relationships of similarity groupings of species than with the differentiations between species. The work is a healthy blend of traditional descriptive taxonomy and of modern numerical taxonomy.

Ten species of Pacific and Indian Ocean ommastrephids form the basis of the study, but 2 Atlantic species, *Illex illecebrosus* and *Ommastrephes pteropus,* were also examined, because no *Illex* (Illicinae) occur in the Pacific and Indian Oceans and because *O. pteropus* is so closely related to *Symplectoteuthis oualaniensis,* which is excluded from the Atlantic. For most species examined, a sufficient number of specimens was available for the numerical analyses to allow a careful selection of specimens to eliminate the variability effects of sex, size, broad geographical range, etc. A broad selection of quantitative characters was examined in each species so that intraspecific variability could be compared with interspecific variability.

The numerical taxonomy consisted of 3 different techniques to examine the species affinities in order to achieve the "best" concept of the interspecific relationships. These included the clustering technique of the weighted variable group method, the recurrent group analysis and the factor analysis. This study represents the 1st major numerical taxonomic analysis to be accomplished on a group of cephalopods, and the results are thought-provoking and interesting.

Lest the use of numerical taxonomy "turns off" the more conservative teuthological

brethren, I hasten to point out that a solid traditional approach presents full species descriptions and synonymies. A number of new characters are introduced, e.g., changes in brachial sucker ring dentition and protective membranes, while other formerly little-used characters are expanded, e.g., fin angle, nape angle. The hectocotyli (mating arm) of *Nototodarus hawaiiensis* and *Dosidicus gigas* are described for the first time. Comments are given for each species on geographical and vertical distributions, habitat, prey-predator relationships, etc.

Although extensive geographical variability is not widespread among most species examined, *Dosidicus gigas* does exhibit a marked latitudinal variation in size in its longitudinally limited range in the eastern Pacific, whereby it grows much larger south of the equator than north of the equator. On the other hand, *Ommastrephes bartrami* has a very broad discontinuous distribution in the Pacific, Indian and Atlantic Oceans with no apparent significant geographical differences.

I feel 2 omissions occur in the descriptive section that detract from a more complete utility of the paper. 1) While good illustrations of the whole animal occur for most, but unfortunately not all, species, no illustrations are given of the distinguishing characteristics. Illustrations in each species of the hectocotylus, the tentacular club and fixing apparatus, and even of the variations in arm and tentacular sucker dentitions would have added to the utility of the paper. 2) The author's stated primary purpose of delineating species affinities not withstanding, a concise comparison of characters for differentiating species would have been most helpful to persons wishing to identify ommastrephids.

A cautionary note is also necessary here. The appearance of tables and distribution charts does not always coincide with the species account in the text, so the reader must check the figure and table legends carefully to avoid mistakes.

The results of the 3 numerical techniques were generally similar in that they divided the species studied into 4 species groups. While these species affinities may raise some traditional eyebrows, they certainly are worthy of consideration, because in some instances at least they seem more justified than are the former groupings. Group A consists of *Symplectoteuthis oualaniensis, Ommastrephes pteropus, Dosidicus gigas* and *O. bartrami*; Group B of *S. luminosa* and *Hyaloteuthis pelagica*; Group C of *Ornithoteuthis volatilis, Illex illecebrosus* and *Todarodes pacificus*; Group D of *Nototodarus hawaiiensis, N. sloani* and *N. gouldi.* Groups A and B show closer affinities to each other, as do Groups C and D. As Wormuth points out, these groups are made up of about half the known species, so a complete analysis at this time is impossible. However, I feel that Groups A (or A and B) and D certainly are reasonable and probably will hang together as discrete units in future analyses, but Group C seems to contain too diverse an assemblage to be natural, in my opinion. It appears as an assemblage in this study because of the species and characters used, but in reality it would break up if all Atlantic species were included and if all pertinent characters were analyzed, e.g., number of rows of suckers on the club (dactylus) in *Illex*. *Illex illecebrosus* and *T. pacificus* may well be ecological counterparts in habitat and behavior in the Atlantic and Pacific Oceans respectively, but a very close taxonomic relationship does not seem justified.

Wormuth presents a revised arrangement of species and genera for the Ommastrephidae strongly suggested by his numerical studies, but he stops short of proposing this as a required taxonomic change. This is much to Wormuth's credit, as he recognizes the necessity of studying all ommastrephid species from all oceans prior to erecting a new system. New generic diagnoses are presented which will provide extremely helpful guidelines to anyone working in the group.

A thorough knowledge of the vertical distributions of ommastrephids is hampered largely by inadequate sampling techniques. Small nets are easily avoided and large nets are seldom fished deep enough to allow determinations of the lower limit of distribution. However,

1500 m certainly appears to approach the maximum depth attained by ommastrephids. Most ommastrephid species are distributed according to particular water masses, and, in general, are divided into oceanic species and neritic species.

This paper is a very detailed and careful piece of work that fills a long-standing need in cephalopod systematics. Given the rate of production of major revisionary works in cephalopod systematics, I judge that Wormuth's publication will form the basis of our knowledge of ommastrephid systematics for many years to come.

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Malacological Review, 1977, 10: 98-183

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THE AMERICAN MALACOLOGICAL UNION, Inc.

BULLETIN

1974

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for 1975

JOINT MEETING of The

Western Society of Malacologists
Eighth Annual Meeting

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Forty First Annual Meeting

San Diego, California

22-26 June 1975

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THE WESTERN SOCIETY OF MALACOLOGISTS

ANNUAL REPORT Formerly "The Echo"

Pomona, California June 19-22, 1974

Dr. Eugene Coan, Editor

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THE WESTERN SOCIETY OF MALACOLOGISTS

Volume 8

ANNUAL REPORT

Joint Meeting With

The American Malacological Union

Special Notice Concerning this Volume

This year, as the result of a joint meeting with the American Malacological Union, members of the WSM and the AMU elected to publish the resulting abstracts and papers solely in the Bulletin of the American Malacological Union. The latter is distributed with the brief WSM Annual Report to members of the Western Society of Malacologists.

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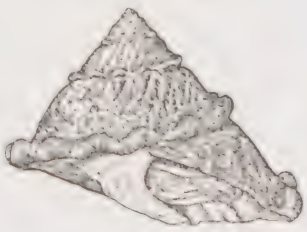

THE WESTERN SOCIETY OF MALACOLOGISTS

ANNUAL REPORT

Volume 9

Pacific Grove, California June 23-26, 1976

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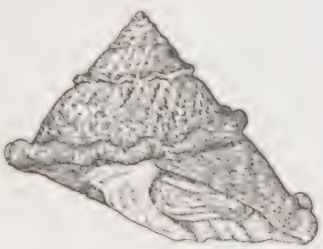

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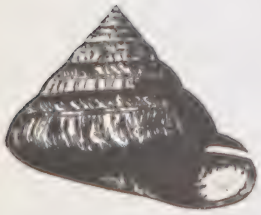

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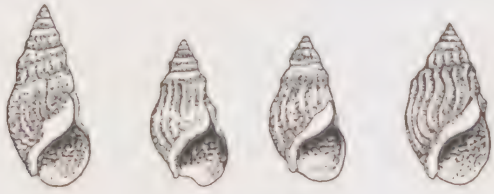

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THE MITRIDAE OF THE WORLD
Part 1. The Subfamily Mitrinae

by WALTER O. CERNOHORSKY

Auckland Institute and Museum
Auckland, New Zealand

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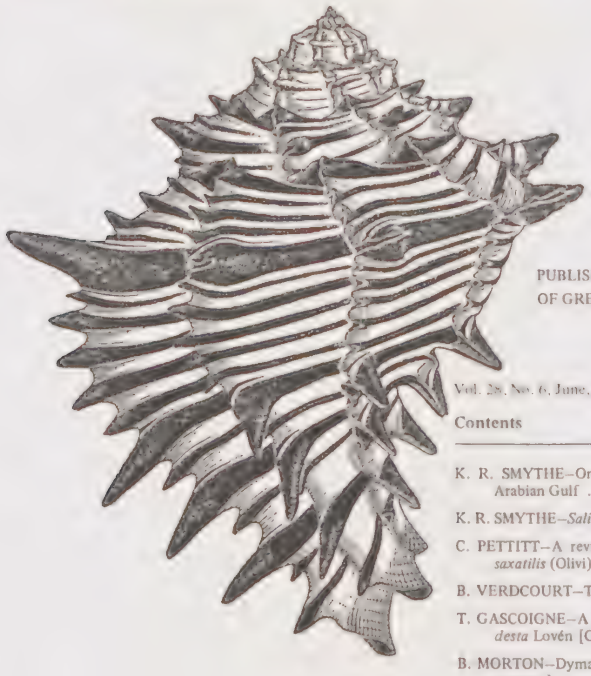

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by

VERA FRETTER and ALASTAIR GRAHAM
Department of Zoology, University of Reading.

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EDITORS
Sara V. Otto and Haskell S. Tubiash
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National Marine Fisheries Service
Oxford, Maryland 21654

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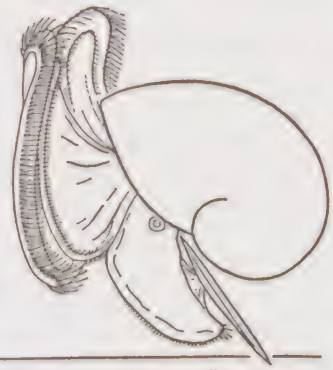

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ORDER, Suborder, DIVISION, Subdivision, SECTION,
SUPERFAMILY, FAMILY, Subfamily, *Genus, (Subgenus)*
New Taxa

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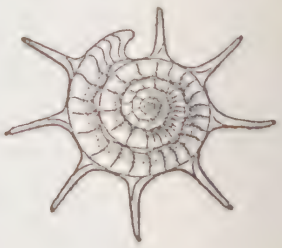

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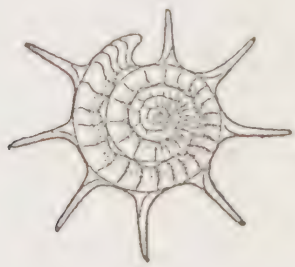

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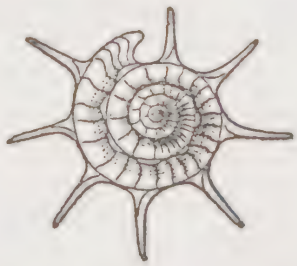

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